CLIMATIC AND NUTRITIONAL CONTROLS ON THE GROWTH OF *EUCALYPTUS GRANDIS* IN SOUTH AFRICA

by

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DECLARATION

I declare that this thesis, submitted for the degree of Philosophy of Science at the University of Witwatersrand, Johannesburg, is the result of my own investigation, unless acknowledged to the contrary in the text. The research has not been submitted before for any degree or examination at any other university.

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ABSTRACT

The upper limit of forest production is constrained by the efficiency of radiation interception and the conversion of carbon dioxide into harvestable products. These processes are limited by water availability and nutrient supply. This study forms part of an international network of experiments aimed at demonstrating the potential yield of a forest species by eliminating water and nutrients as growth-limiting factors. The main aim of this study was to determine the climatic and nutritional controls on the growth of *Eucalyptus grandis* under a given set of environmental conditions. A field experiment was initiated in the KwaZulu-Natal Midlands, South Africa, to establish the effects of varying levels of water and nutrient availability on the physiological processes controlling tree growth in *E. grandis*. The experimental design consisted of a control (C), irrigation (I), fertilisation (F), and irrigation and fertilisation (IF) treatments. These treatments aimed to eliminate both water (I and IF) and nutrients (F and IF) as growth-limiting factors. The study focused on three main areas, namely tree-water relations, nutrient dynamics and acquisition, and carbon allocation. Information on these processes was acquired through a combination of field data collection, the application of foliar diagnostic tools, and a modelling approach.

The growth of the *E. grandis* trees in this trial was constrained by poor establishment and management practices. Inadequate vegetation control and vigorous weed growth were a source of competition during the establishment of the seedlings. In addition, the variable seed stock, late fertiliser application and damage from animals resulted in late canopy closure. Consequently, the potential growth of *E. grandis* at this site could not be determined, and comparisons were made between the different treatments rather than demonstrating maximum growth under optimal conditions.

The biomass and nutrient pools were quantified to provide a mid-rotation value of the nitrogen (N) and phosphorus (P) contents contained in the soil, forest floor and above- and below-ground biomass. At age four years, irrigation had a more pronounced effect on growth and biomass accumulation than fertilisation. Increases in diameter, height, basal area, standing volume and above- and below-ground biomass were observed in response to increased water availability. After four years, the respective totals of the above- and below-ground biomass pools accumulated by the C, I, F and IF treatments were 73, 82, 78 and 85 t ha^{-1}. In irrigated (I and IF) treatments, significantly more above-

ground biomass was allocated to the stem, compared to non-irrigated (C and F) trees. The lower root:shoot ratio in fertilised (F and IF) trees indicated that proportionally less mass was allocated to below-ground components compared to non-fertilised (C and I) trees. Irrigated trees accumulated more N and P than non-irrigated trees in above- and below-ground biomass fractions.

The 3-PG model has shown considerable potential as a tool for predicting forest productivity. As part of a model validation exercise, 3-PG was applied to this stand. Simulations were run over a two-year period using appropriate initialisation data and a parameter set developed for *E. grandis* in the summer rainfall region of South Africa. The model was validated using observed leaf area index (*L*) and foliage and above-ground woody biomass, and then used to predict stand volume. The 3-PG model produced accurate predictions of *L*, foliage and above-ground woody biomass. At four years, the model-predicted *L* over all treatments ranged from 3.8 to 5.0, in contrast to the observed range of 4.3 to 5.2. Stand volume at four years of age was under-estimated in the non-irrigated treatments. Actual stand volume at this age ranged from 100 to 118 m^3 ha^{-1} across all treatments, compared to model estimates of 82 to 123 m^3 ha^{-1}. The 3-PG model can be used as a guide for future research direction, which should focus on a better understanding of nutritional dynamics operating at a site. Use of a dynamic fertility rating may improve model predictions and there is possible scope for improvement in the water-balance component of the model. Results from this study have shown 3-PG to be a robust model by producing accurate predictions of growth under varying levels of resource availability.

There is much current interest in predicting the maximum amount of water that can be transpired by *Eucalyptus* trees. It is possible that industrial waste water may be applied as irrigation water to eucalypts and it is important to predict the maximum transpiration rates of these plantations in an attempt to dispose of this contaminated water. A simple model was developed to predict maximum rates of daily transpiration by short-rotation *E. grandis* plantations experiencing no significant soil water deficits or fertility limitation. Daily sap flow data recorded in a single average tree in the irrigated treatment were used to estimate mean daily canopy conductance. Analysis of daily and seasonal variation in conductance confirmed that solar radiation and vapour pressure deficit are the dominant factors reducing canopy conductance below potential values, when soil water availability is high. A simple canopy conductance model based on these data was then used with the Penman-Monteith equation to predict daily transpiration rates by *E. grandis* trees at a second site situated in Mpumalanga. The modelled transpiration rates agreed well with the observed daily sap flow (R^2 = 0.79). The total observed annual sap flow at the Mpumalanga site was equivalent to 1320 mm compared to the modelled value of 1226 mm.

Fertilisation is one of the most cost-effective methods of increasing and maintaining the productivity of *E. grandis* plantations in South Africa. This silvicultural practice can be optimised by using the foliar nutrient ratios measured in plants at maximum growth as a guideline for fertiliser application. The foliar ratios present at optimum growth are similar across a wide range of plant species and can be defined in relation to N. A study was conducted to determine whether the proportions of elements relative to N could be refined specifically for *E. grandis* through the use of diagnosis and recommendation integrated system (DRIS) norms. The DRIS norms for N, P, potassium (K), calcium (Ca) and magnesium (Mg) were derived from published studies on *E. grandis* and compared to the target values recommended by Linder (1995) for optimal growth. The DRIS norms for P and K relative to N corresponded to the target values, but the Ca:N and Mg:N ratios were much higher, indicating luxury consumption of these elements. A similar trend was observed for foliar nutrient ratios calculated from published data on a wide range of plant species. The DRIS appears useful for diagnosing the nutrient status, provided accurate DRIS norms are used and indices are interpreted correctly. In most cases, the diagnosis made using the DRIS indices was confirmed with the optimal ratio approach. Diagnoses made using these techniques indicated that foliar P and K concentrations were sub-optimal at age four years.

The results from this trial suggest that there was an apparent temporal separation of resource limitation experienced at this site. Initially, the trees appeared to be constrained by nutrient availability, whereas water was potentially more limiting to growth than nutrient supply at age four years. However, it is highly unlikely that irrigation of forest species would ever be implemented on an operational scale in this country. Rather than pursuing the potential responses that could be obtained with unlimited water availability, the forest industry in South Africa would benefit greatly from improved fertiliser recommendations. On the basis of the optimal foliar technique and the DRIS approach, foliar ratios of 100 N: 8 P: 35 K: 2.5 Ca: 4 Mg are suggested for optimal growth of *E. grandis* trees.

DEDICATION

To the loving memory of Shaun Philip Wilshire,
On whose wings I first learnt to fly.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 SOUTH AFRICAN PLANTATION FORESTRY

South Africa has emerged as a major contender in the global forest market in the last two decades. The forest industry makes a significant contribution to the national economy; benefits gained from this sector include employment, contribution to the national GDP, provision of household livelihoods, especially in rural areas, and the acquisition of foreign exchange due to export earnings (DWAF, 1997). In addition, this country is regarded as the world leader in forest certification (FSA, 2004). To ensure that South African timber supply not only continues to meet domestic demand, but that this sector maintains its importance in an international context, sustainable gains in timber volume must continue. The total roundwood timber produced annually from the 1.4 million hectare (ha) plantation area is 19.2 million m^3 (DWAF, 2004). The projected consumption for 2020, however, is calculated to approximate 37.1 million m^3 (DWAF, 1997). The common response to the anticipated increase in demand for forest products is to expand the plantation area. However, further afforestation may be limited by restrictions such as permits and availability of suitable land and water resources. Catchments that were originally covered with grassland have been converted to predominantly pine and eucalypt plantations. These exotic species are preferred for afforestation because none of the indigenous tree species which yield useful timber grow at rates considered to be profitable (Grut, 1965).

Eucalyptus grandis, which is indigenous to Australia, is grown predominantly for pulpwood and mining timber, and is the most widely planted hardwood in South Africa, accounting for approximately 23% of the total plantation area (DWAF, 2004). The harvested tree stump of *E. grandis* coppices to form second and more crops, which are normally harvested between seven and ten years (The South African Forest Owners Association, 1997). Productivity from these plantations is relatively high and ranges from approximately 17 – 52 m^3 ha^{-1} yr^{-1}. The high growth rates and success of this species can be attributed to the deployment of high quality genetic material and intensive silvicultural management regarding site preparation, correct site-species matching, good establishment practices, optimum planting density, appropriate vegetation control, and adequate nutrition.

Increasing the productivity of new and existing plantations can partially compensate for the deficit in new afforestation (Schönau, 1983). Due to the importance of *E. grandis* in this country, suitable management regimes must be implemented to ensure these plantations generate high levels of productivity on a sustainable basis. One such approach frequently adopted in South Africa is fertiliser application, which has been shown to be one of the most cost-effective methods of economically improving and maintaining productivity of commercial plantations (Schönau, 1983; Herbert and Schönau, 1989). The expected increase in timber volume with fertilisation of eucalypts is proportional to site quality, and conservative estimates range from 30 – 60 tonnes of air-dry timber per ha over an eight to ten year rotation period (ICFR, 2000). Rapid growth rates that result in trees attaining a merchantable timber size over a shorter time period also result in higher amounts of nutrients being removed from the site during a harvesting operation (Herbert, 1992). This could, potentially, cause problems for sustainable productivity. In addition, the conversion of grassland to forest plantations has sparked concern over the effects of these changes on water resources (Dye and Olbrich, 1993). A deeper understanding of long-term water balance is necessary to determine the sustainability of continuous eucalypt cropping (Dye *et al*., 1997). Consequently, the South African forest industry considers improving the predictions of growth and water use in forest plantations as an important research goal (Dye *et al.*, 2004). Estimates of growth and yield are commonly made using empirical growth models. These models are insensitive to changes in environmental or management conditions, and are therefore limited in their applications. In contrast, process-based models can be used to assist in identifying factors which limit growth, to evaluate the biological consequences of management decisions, and to explore the effect of different silvicultural practices on the utilisation of site resources (McMurtrie *et al*., 1990).

Water availability and nutrient supply are the most common factors which limit the productivity of plantation forest growth (Brown *et al*., 1997). Tree growth is driven by the interception of radiation and the efficiency with which leaves use this energy to produce biomass through the process of photosynthesis (Landsberg, 1997). Leaf area index influences productivity through the interception of light and is a pivotal integrator of water availability and productivity of a stand (Gholz *et al*., 1990). This sensitivity of L to the water regime occurs because the transpirational surface area is directly affected by changes in leaf area (Gholz *et al*., 1990). The *L* that can be maintained at a given site will be determined by the availability of water and nutrients (Beadle, 1997). Generally, nutrient limitations are overridden by climatic constraints, as even trees in a very fertile soil will not grow under limited water supply or when temperature is unfavourable (Landsberg and Waring, 1997).

Many long-term experiments were initiated in Sweden during the late 1960's to determine the primary production of forest ecosystems at optimum nutrient levels (Linder, 1995). These experiments included repeated additions of N and other nutrient elements. Nitrogen regulates the development of foliage, which controls plant production, and therefore the extent of wood increment (Schönau and Herbert, 1989). These types of experiments enable a relationship to be established between tree nutrition and forest yield (Linder, 1995). These studies were further developed into nutrient optimisation trials which aimed to determine the effects of 'near-optimal' water and nutrient availability on the growth of forest trees.

The production ecology of eucalypt species has been investigated in Brazil and Hawaii (Binkley and Ryan, 1998; Giardina and Ryan, 2002; Stape, 2002; Binkley *et al*., 2004; Gonçalves *et al*., 2004; Stape *et al*., 2004a). These studies investigated the ecophysiological processes (e.g. canopy light interception and photosynthesis, water relations and carbon allocation patterns) controlling the potential productivity of tropical *Eucalyptus* plantations. Although resource supply was the main focus of these studies, the results indicated that resource capture and resource use-efficiency were the key components defining production, and that these efficiencies were under strong water-supply influence (Stape *et al*., 2004a). The most productive stands used more water, light and N, but were also the most efficient in using these resources, possibly due to a combined effect of high carbon assimilation rates and above-ground carbon allocation (Stape *et al*., 2004a). In fertilised tropical *Eucalyptus* plantations, water is the most important resource controlling potential productivity due to its influence on canopy quantum efficiency and *L* (Stape, 2002).

Despite the application of intensive silvicultural operations (Schönau, 1984) and 50 years of fertiliser research in South Africa, we have limited understanding of how the availability of growth resources, mediated through these practices, influences the underlying physiological processes determining tree growth. The response mechanism of *E. grandis* to increases in soil water and nutrient availability was investigated by du Toit and Dovey (2005). These authors addressed the effects of intensive site management operations on resource availability in a young eucalypt stand in KwaZulu-Natal, South Africa. Initial leaf area development responded strongly to a nutrient availability gradient produced by site management treatments (du Toit and Dovey, 2005). Wood production was driven by increases in *L* rather than increases in photosynthetic efficiency or growth efficiency (woody biomass produced per unit leaf area) (du Toit and Dovey, 2005).

1.2 APPROACH TO THE STUDY

The approach adopted in this study was to implement a trial to establish the effects of varying levels of water and nutrient availability on the physiological processes controlling tree growth in *E. grandis*. The primary aim of this study was to determine the climatic and nutritional controls on the growth of this species under a particular set of South African environmental conditions. The experimental design consisted of an untreated control (C), irrigation (I), fertilisation (F), and irrigation and fertilisation (IF) treatments. The purpose of acquiring these results was to demonstrate potential forest yields by adjusting water (I and IF) and nutrient supply (F and IF) to uptake requirements. The study focussed on three main areas, namely tree-water relations, nutrient dynamics and acquisition, and carbon allocation. Information on these processes was acquired through a combination of field data collection, the application of foliar diagnostic tools, and a modelling approach. In this study, foliar analysis was used as the basis for fertiliser recommendations: an optimal foliar N status was defined, and target values were set for each nutrient element relative to N.

1.3 OBJECTIVES

The following objectives and key questions were proposed:

Objective 1: To determine the relative importance of water and nutrition in limiting growth at this particular site.
Key Question 1: To what extent is the growth of *E. grandis* controlled by climate (water supply) and site (nutrition) constraints, and does this change with time?

Objective 2: To quantify the biomass and N and P pools contained in the soil, forest floor and above- and below-ground components of *E. grandis* trees subjected to varying levels of irrigation and fertilisation.

Key Question 1: How do the different irrigation and fertilisation treatments affect above- and below-ground biomass production and partitioning in these components?

Key Question 2: How do varying levels of water and nutritional constraints influence the N and P pools contained in the above- and below-ground fractions of an *E. grandis* stand?

Objective 3: To validate the 3-PG model using a parameter set developed for *E. grandis* for the summer rainfall region of South Africa, by applying the model to biomass data collected from this irrigation and fertilisation trial.

Key Question 1: Is it possible to predict above-ground biomass production, *L* and volume in a young *E. grandis* stand subjected to varying levels of water and nutritional constraints using a process-based model?

Objective 4: To quantify the water use of *E. grandis* trees growing under conditions of non-limiting soil water availability using sap flow measurements and the Penman-Monteith equation.

Key Question 1: Can a simple model, using standard weather data, be constructed to predict canopy conductance?

Key Question 2: How well does the canopy conductance model predict daily transpiration rates at a second site?

Objective 5: To manipulate and improve the proportions of elements relative to N by diagnostic foliar analyses.

Key Question 1: Can diagnostic foliar analyses be used to manipulate and improve the proportions of elements relative to N in the fertilised trees?

Key Question 2: Can the proportions of elements relative to N be refined for *E. grandis* through the use of diagnostic and recommendation integrated system (DRIS) norms?

It was hypothesised that

- Growth is constrained more by water availability than nutrient supply.
- Increased water and nutrient supply will result in higher growth rates due to increased *L* and allocation of biomass to stems.

- On the basis of diagnostic foliar analyses and repeated fertiliser applications, optimal nutrient status can be created and maintained in fertilised (F and IF) trees.
- Biomass production will be increased by maintaining the proportions of elements relative to N at an optimum rather than by maintaining high concentrations of individual elements.

1.4 STRUCTURE OF THE THESIS

The research presented in the following chapters addresses these objectives and the respective key questions. This chapter served as a general introduction to the thesis, and is followed by a literature review (Chapter 2), which includes the key references that provide a theoretical background to the study. Chapter 3 sets the scene for the research by describing the study site and experimental design. Some of the limits and constraints experienced with long-term experiments are highlighted. Results are presented in Chapters 4 – 8, which have been produced as a series of scientific papers. These results appear in the text in very similar forms to the individual papers that have either been published or submitted for publication. As such, some material has been repeated in the thesis, particularly in the introduction and conclusion sections. The published papers are included in Appendix 2. A general discussion on the climatic and nutritional constraints on the physiological processes controlling the growth of *E. grandis* is given in Chapter 9. The overall conclusions are presented in Chapter 10, followed by the reference list in Chapter 11.

CHAPTER 2

LITERATURE REVIEW

2.1 ACQUISITION OF GROWTH RESOURCES AND DRY MATTER PRODUCTION

2.1.1 Radiation Interception and Photosynthesis

Forest production is driven by radiation interception and the efficiency with which trees use this energy to convert carbon dioxide (CO_2) into woody biomass through the process of photosynthesis (Linder, 1985; Linder *et al.*, 1985; McMurtrie *et al.*, 1990; Landsberg and Hingston, 1996; Landsberg, 1997; Binkley *et al.*, 2004). High levels of intercepted radiation are associated with high levels of productivity (Rook, 1985); a linear increase in biomass production with the amount of radiation absorbed by the foliage has been demonstrated for agricultural crops (Monteith, 1977) and forest stands (Linder, 1985). Radiation interception and the uptake rate of CO_2 depend on leaf area (Landsberg, 1986a). Environmental and site constraints that have a primary influence on leaf area production (e.g. water deficits, reduced N availability or sub-optimal temperatures) influence the growth rate through their effects on radiation interception (Jarvis and Leverenz, 1983) and the efficiency with which intercepted radiation is assimilated (Rook, 1985).

Photosynthetic efficiency is influenced by the foliar nutrient status, and also depends on the uptake of CO_2 through the stomata, which may be affected by the water status of the leaves (Landsberg, 2003a). Nitrogen fertilisation plays a key role in plantation establishment and growth, through effects on leaf area and the photosynthetic capacity of the foliage (Landsberg, 1986a; Pereira *et al.*, 1996). During the early stages of stand establishment, most of the nutrients required for growth are taken up from the soil. Once the stage of canopy closure is reached, a substantial amount of the nutrient requirement is met by biochemical cycling (Fife and Nambiar, 1982; Ericsson, 1994a), and nutrient uptake following fertilisation may not increase as much as in a young plantation (Landsberg, 1997). According to Linder and Rook (1984), a significant increase in production following fertilisation can be achieved in hardwood species, due to an improved rate of photosynthesis per unit leaf area, even after canopy closure. An increase in *L* that occurs in many forest stands after fertilisation, especially with N, results in an increased transpiration rate at the tree and stand level (Linder and Rook, 1984). The increases in total transpiration and interception losses (resulting from higher *L*) may, through increasing water deficits, indirectly affect photosynthesis (Linder and Rook, 1984).

2.1.1.1 Forest productivity models

Virtually all process-based models of forest productivity are based on the radiation intercepted by canopies, and the subsequent conversion of this radiation into carbohydrates (Landsberg and Gower, 1997). These types of models describe forest productivity in terms of the physiological processes that control plant growth, i.e. photosynthesis, respiration, nutrition, carbon allocation, transpiration and litterfall. Process-based productivity models are viewed by the South African forest industry as potentially useful tools for improving growth and water-use predictions of forest plantations (Dye *et al*., 2004).

One such model, 3-PG, has shown considerable potential as a tool for predicting forest productivity. This model has yielded credible predictions for a wide range of species growing under different climatic conditions in Australia and New Zealand (Landsberg and Waring, 1997; Coops *et al.*, 1998; Sands and Landsberg, 2002), Brazil (Almeida *et al.*, 2004a; Stape *et al.*, 2004b), Chile (Rodríguez *et al.*, 2002), USA (Coops and Waring, 2001; Landsberg *et al.*, 2001), South Africa (Gush, 1999; Dye, 2001; Esprey and Smith, 2002; Dye *et al.*, 2004), and Sweden (Landsberg *et al.*, 2003).

3-PG is a simple process-based stand-level model of forest growth which requires only readily available site and climatic data as inputs (Sands and Landsberg, 2002; Landsberg, 2003b). This model is based on the fraction of photosynthetically active radiation absorbed by the forest canopy, calculated using Beer's Law (Landsberg and Waring, 1997). In 3-PG, the conversion of absorbed photosynthetically active radiation to gross primary production (GPP) is based on a theoretical maximum canopy quantum efficiency constrained by various environmental modifiers (atmospheric vapour pressure deficit (*D*), available soil water, mean air temperature, frost, site nutrition and stand age; Sands and Landsberg, 2002). Net primary production (NPP) is calculated as a constant fraction of GPP, which is then allocated to roots, stems and foliage (Landsberg *et al.*, 2001). The proportion of NPP allocated to roots increases if nutritional status and/or available soil water are low, and allocation to stems and foliage is reduced such that the allometric balance of the trees is conserved (Landsberg and Waring, 1997; Landsberg *et al.*, 2001). The 3-PG model predicts the time course of NPP, above- and below-ground biomass pools, and available soil water and stand transpiration, computed using the Penman-Monteith equation (Landsberg and Waring, 1997). Model outputs of interest to the forest manager are mean stem diameter, *L*, stand volume and mean annual increment (Sands and Landsberg, 2002).

2.1.2 Nutrient Acquisition, Carbon Allocation and Water Relations

The timber yield of a forest crop is determined by the rate of canopy photosynthesis and the allocation of photosynthate to stem growth (McMurtrie *et al*., 1990). These processes are strongly influenced by the supply of water and nutrients (Linder and Rook, 1984; McMurtrie *et al.*, 1990). Silvicultural practices such as site preparation, irrigation, fertilisation and vegetation control (Wise and Pitman, 1981) can alter the levels of available water and nutrients, thereby increasing the *L* and hence productivity of a stand (Beadle, 1997).

2.1.2.1 Nutrient acquisition and carbon allocation

The quantity of nutrients taken up by trees is influenced by soil processes which regulate nutrient quantities in the soil solution, the amount and distribution of fine roots and mycorrhizas (Landsberg and Gower, 1997), the soil moisture status, the efficiency of nutrient absorption from the soil, the total nutrient demand of the stand, the growth rate of the trees, and the efficiency with which trees use nutrients for growth (Gonçalves *et al.*, 1997). The dry matter distribution between roots and shoots of forest species is determined by the genetic constitution of the trees (Ericsson, 1994a), site quality (Santantonio, 1989), tree age and season (Ericsson *et al.*, 1996), mineral nutrition (Linder and Rook, 1984; Ågren and Ingestad, 1987; Ericsson, 1994a), water availability (Axelsson and Axelsson, 1986; Fabião *et al.*, 1995) and silviculture (Misra *et al.*, 1998a). In nutrient-limited or dry environments, relatively more dry matter and nutrients are contained in below-ground components of eucalypts than on moist, high-nutrient sites (Grove *et al.*, 1996).

The root:shoot functional equilibrium referred to by Cannell (1985) is plastic, where assimilates are allocated to shoots under conditions that limit photosynthesis (low supply of light or CO_2), or to roots if water or nutrient availability are limited (Ericsson *et al.*, 1996). However, the response to nutrient deficiencies is not uniform, as plants limited by N, P or sulphur allocate more resources below-ground compared to those deficient in K, Mg, iron (Fe) or manganese (Mn), which exhibit poor root growth (Ericsson *et al.*, 1992).

Improvements in silviculture may affect biomass production by increasing the growth of above- and below-ground parts (either with or without a change in the ratio of these components), or by favouring production of one component at the expense of the other, which would not result in an apparent increase in total biomass (Misra *et al.*, 1998a). When water is not limiting, improved nutrition normally results in an increased proportion of NPP allocated to above-ground parts (Landsberg and Waring, 1997). This type of allocation pattern has previously been explained by increases in foliage biomass or photosynthetic rates (Axelsson and Axelsson, 1986), but it is uncertain whether this response is caused by an increase in total productivity, a shift in allocation from below- to above-ground, or a combination of these factors (Keith *et al.*, 1997). Improved water and nutrient availability have been reported to reduce below-ground biomass allocation (Linder and Rook, 1984; Axelsson and Axelsson, 1986; Ågren and Ingestad, 1987; Fabião *et al.*, 1995; Albaugh *et al.*, 1998; Stape, 2002), which would result in more carbohydrates for stem growth (Binkley, 1986).

2.1.2.2 Long-term nutritional sustainability

Implementing silvicultural operations that increase site resources would result in trees attaining a merchantable timber size over a shorter time period (Herbert, 1992). The rapid growth rate of high-yielding plants makes them nutrient demanding, given the closely-linked processes of growth and nutrient uptake (Ericsson, 1994b; Gonçalves *et al.*, 1997). The high nutrient accumulation of such fast-growing plantations, in combination with shorter rotation periods, can potentially impact the long-term sustainability of productivity (Attiwill and Leeper, 1987; Herbert, 1992; Ericsson, 1994a; Judd, 1996; Santana *et al.*, 2000; Hunter, 2001).

The construction of nutrient budgets is the most common method for determining the effects of harvesting on productivity (Judd, 1996). Nutrient budgets contrast the balance between input and output fluxes with the amount of nutrients in the soil and therefore provide pertinent information for decision making on long-term nutrient supply (Fölster and Khanna, 1997). Nitrogen and P are the two elements most frequently limiting to forest growth (Pritchett, 1979; Grove *et al.*, 1996; Fölster and Khanna, 1997). Concern surrounding long-term sustainability of plantation productivity with respect to these potentially limiting elements has resulted in the construction of N and P budgets for *Eucalyptus* stands (e.g. Judd, 1996; Santana *et al.*, 2000; du Toit and Scholes, 2002; du Toit, 2003). The impacts of high-yielding short rotations on sites in South Africa are not well documented or understood (Herbert, 2003).

2.1.2.3 Water relations

Higher growth rates resulting from intensive silvicultural practices tend to increase water consumption (Ericsson, 1994a). The water use of exotic plantations in South Africa is a controversial issue because intensively afforested areas co-incide with crucial catchments (Olbrich *et al*., 1993). As South Africa is a water-limited country, there is intense competition between potential water users for this limited resource (Olbrich *et al*., 1993). Information is required on the water consumption of plantations as compared to alternative vegetation so that water resources can be equally allocated among all users (Dye and Olbrich, 1993). The rates of water use by *E. grandis* are documented in many studies (e.g. Dye, 1987; Dye and Olbrich, 1993; Olbrich *et al*., 1993; Dye, 1996; Myers *et al*., 1996; Dye *et al*., 1997; Kallarackal and Somen, 1997a; Soares and Almeida, 2001). Despite this information, there are still insufficient data to predict the water use of this species over the broad range of growing conditions.

Transpiration rates are influenced by atmospheric evaporative demand, soil moisture availability, and canopy conductance, which in turn is controlled by stomatal conductance and leaf area (Waring and Schlesinger, 1985; Beadle, 1997; Landsberg and Gower, 1997). The three predominant environmental controls on stomatal conductance at the canopy level are light intensity, *D*, and the water status of the leaves (Landsberg and Gower, 1997). Stomatal conductance forms the link between transpiration and photosynthesis by controlling the flux of CO_2 into, and water vapour out of the leaves (Landsberg and Gower, 1997). Stomata normally open at high air humidity and with increasing radiation, but close under high CO_2 concentrations and as the *D* increases (Landsberg, 1997). A consequence of stomatal closure, however, is reduced CO_2 uptake, and therefore decreased growth rates (Landsberg and Gower, 1997;

Landsberg, 2003a). At low levels of available water, where stomatal closure is induced, canopy conductance and transpiration also decline (Beadle, 1997).

Models have been developed to describe the response of stomatal and/or canopy conductance to two of the major environmental influences, light and *D* (Thorpe *et al*., 1980; Warrit *et al*., 1980; Kaufmann, 1982a,b; Dye and Olbrich, 1993; Granier *et al*., 2000). Model estimates of canopy conductance are frequently used in combination with the Penman-Monteith equation (Monteith, 1965, 1981) to predict transpiration rates (Dye, 1987; Green, 1993; David *et al*., 1997; Landsberg and Waring, 1997; Soares and Almeida, 2001). This equation combines the two environmental drivers of evaporation, i.e. net radiation and dryness of the air, with a physical control (boundary layer conductance), and a physiological control (canopy stomatal conductance) (Landsberg and Gower, 1997; Waring and Running, 1998).

Pre-dawn water potential measurements provide a valuable assessment of the effects of water status on growth (Landsberg, 1997). Nocturnal equilibration of xylem water potential normally occurs as water moves to those areas surrounding the roots from which it was absorbed the previous day (Landsberg and Gower, 1997). Pre-dawn water potential measurements are used to represent the diurnally least-stressed condition of plant water status, based on the assumption that these values approximate the soil water potential (Landsberg, 1986a; Myers and Talsma, 1992; Landsberg and Gower, 1997).

2.2 NUTRIENT STATUS AND FOLIAR DIAGNOSTIC TOOLS

2.2.1 Nutrient Status

The nutrient status at a site can be assessed through soil or plant tissue analyses. Soil analyses are most useful before planting, to determine nutrient availability to the plant, and to provide recommendations on the amounts of fertiliser to be applied (Mead, 1984). Once trees have been established, plant tissue analysis, particularly foliar analysis, is the preferred method of evaluating plant nutrient status as it provides an integrated assessment of all the factors that influence nutrition (Ulrich and Hills, 1967; Needham *et al*., 1990), such as nutrient supply, plant uptake, translocation and growth (Richards and Bevege, 1972). Foliar analysis has the advantage of being directly related to productivity as foliage is the site of photosynthesis (Mead, 1984). Accordingly, correctly interpreted plant analyses may aid in identifying nutrient deficiencies and imbalances which could lead to a loss of potential production or a decline in productivity (Melsted *et al.*, 1969).

In South Africa, plantation eucalypts growing on highly-weathered soils of low nutrient status often exhibit a healthy appearance and very rapid growth rates where the climatic conditions and soil physical characteristics are favourable (Schönau and Herbert, 1989). Consequently, foliar rather than soil analysis is considered more appropriate for determining the nutrient status of a site (Herbert, 1996). Foliar analysis is a generally accepted and commonly used tool to diagnose the nutrient status of trees (Ballard, 1978; Ingestad, 1979a,b, 1981; Lea and Ballard, 1982; Ericsson, 1994c; Linder, 1995; Dell, 1996; Herbert, 1996; Judd *et al.*, 1996a). Research into fertilising eucalypts in South Africa has benefitted particularly from the application of foliar analysis (Schönau, 1983). In the summer rainfall areas of South Africa, severe nutritional disorders are uncommon, and nutrient balance and the order of limiting nutrients becomes important (Herbert and Schönau, 1990). Accordingly, foliar analysis has been used particularly to determine the effectiveness of fertiliser application and examine nutrient balances within the tree, rather than identify critical foliar levels below which growth is seriously curtailed (Herbert, 1992, 1996). The ratios between N, P, K, Ca and Mg give a clearer and more direct indication of the fertiliser requirements and nutrient status of eucalypts than the concentrations of these individual elements (Schönau, 1982; Schönau and Herbert, 1983). The best growth is achieved when there is an overall balance of nutrients, i.e. where the nutrient ratios all approach their optima (Herbert, 1992, 1996).

2.2.2 Foliar Diagnostic Tools

The diagnostic techniques commonly used to assess plant nutrient status include the critical level approach (Ulrich, 1952; Ulrich and Hills, 1967; Melsted *et al.*, 1969), vector analysis (Timmer and Stone, 1978), optimum nutrient ratios (Ingestad, 1979a,b, 1981, 1987; Ericsson *et al.*, 1992; Ericsson, 1994c; Linder, 1995), the diagnosis and recommendation integrated system (DRIS; Beaufils, 1971, 1973), and the deviation from optimum percentage (DOP) index (Montañés *et al.*, 1993). Each of these approaches are briefly reviewed.

2.2.2.1 The critical level approach

The critical level is defined as that nutrient concentration associated with a 10% reduction in yield (Ulrich and Hills, 1967; Richards and Bevege, 1972). According to Ulrich (1952), however, the critical level is not a single data point, but a narrow range of nutrient concentrations, above which luxury consumption, and below which deficiency, and growth limitation (Melsted *et al.*, 1969) occur. Critical levels are influenced by factors that may confound the nutrient concentrations measured in plants, such as age (Ulrich, 1952), season, position in the crown, extent of crown closure, moisture stress (van den Driessche, 1974), starch content (Pereira *et al.*, 1989, Ericsson *et al.*, 1992; Linder, 1995), and the extent of nutrient retranslocation (Fife and Nambiar, 1982; Nambiar and Fife, 1987). The critical level concept requires that the plant tissue under investigation be compared with the critical level determined at the same physiological stage (Sumner, 1977a,b,c). In this approach, it is assumed that no nutrients are limiting, except for the one being tested, and these levels can only be utilised accurately if this condition is met (Richards and Bevege, 1972).

2.2.2.2 Vector analysis

Vector analysis is a technique that associates nutrient status and growth response with research or operational practices (Haase and Rose, 1995). The vector analysis approach enables comparison of multiple treatment effects relative to an untreated (reference) status (Haase and Rose, 1995). Using this approach, nutrient content, concentration and foliar mass (or an appropriate surrogate thereof) are plotted as vector diagrams. Vectors, drawn from the reference point to each of the plotted treatment data points, indicate the relative shifts in nutrient content, concentration and dry mass as compared to the control. Vector magnitude reflects the severity of the diagnosis, i.e. the longest vector is associated with the most responsive nutrient or treatment (Haase and Rose, 1995). As it is a comparative technique, vectors can be interpreted free from pre-determined critical values or ratios (Haase and Rose, 1995). Identification and interpretation of nutrient dilution, nutrient interactions (Timmer and Armstrong, 1987) and luxury consumption, which may be difficult using conventional diagnostic approaches, is simplified by vector analysis (Timmer and Stone, 1978).

2.2.2.3 Optimum nutrient ratios

The nutrient balance approach can be viewed as an extension of the critical nutrient theory (Ulrich, 1952). In nutrient balances, the proportions of the elements in the foliage, as well as the actual concentration are assessed (Ulrich, 1952). Ingestad (1979a,b, 1981) adopted a similar approach to the nutrient balance concept to maintain optimum nutrition in tree seedlings. In this technique, nutrients are added in fixed proportions to N found present in plants at maximum growth. The internal nutrient proportions required for maximum growth are similar across a wide range of species (Ingestad, 1987). This is not surprising considering that all plants share the same basic physiological processes such as photosynthesis, respiration, cell division and the production of associated enzymes (Ericsson *et al*., 1992; Ericsson, 1994a). Linder (1995) used the optimum ratio approach to detect and correct nutrient imbalances, and maintain optimal nutrient status in Norway spruce (*Picea abies*) trees. Target values were set for the foliar nutrient concentrations of each element, based on results obtained from laboratory studies and long-term forest nutrition experiments, in which plant nutrient requirements were established (Linder, 1995). According to foliar analysis and predicted growth response, the quantities of nutrients to be applied were estimated in relation to the target value (Linder, 1995). The optimal nutrient ratio technique is based on the following assumptions:

- Over a wide concentration range, the proportions of elements relative to N are at least as, if not more important than the absolute nutrient concentration;
- Optimal growing conditions can only occur if all essential nutrients are present in the correct proportions, and
- Optimal nutrient element proportions are similar for all higher plants and can be defined relative to N (Linder, 1995).

2.2.2.4 The diagnosis and recommendation integrated system (DRIS)

The optimal nutrient ratio and DRIS techniques are fundamentally similar. In the DRIS approach, any factor that potentially influences yield (e.g. soil properties, climatic conditions, management practices and plant composition) must be identified, and the relationships existing between these factors and yield must be defined (Beaufils, 1973). The established relationships are expressed as diagnostic indices which form calibrated norms, used for diagnosis and recommendation purposes (Beaufils, 1973). The DRIS incorporates the concept of nutrient balance by identifying the most limiting nutrient and ranking the order in which other nutrients may potentially limit yield (Sumner, 1977a,b,c, 1979).

Jones (1981) summarises the several assumptions on which the DRIS is based:

- Ratios of nutrient elements are often superior indicators of nutrient status than single elemental concentrations,
- Some nutrient ratios are more important than others,
- Maximum yields can only be attained when nutrient ratios approach an optimal value; deviations from this value result in lower growth,
- A ratio used in the calculation of a DRIS index should have a significantly higher variance in the low-yield sub-population compared to the high-yield sub-population, and
- A DRIS index is the mean deviation of a ratio from its optimum value – the optimum DRIS index would be zero, with negative indices indicating relative nutrient deficiencies and positive indices, relative sufficiency or excess.

The relative order and magnitude of these indices are important for diagnostic purposes (Beaufils, 1973). The nutritional balance index (NBI) is calculated as the sum of the absolute values of all the DRIS indices and can be used as a measure of the total nutritional balance for the elements examined (Elwali and Gascho, 1984). The higher the NBI value, the greater the nutritional imbalance.

Application of the DRIS approach can minimise sampling restrictions (in terms of plant age and position of the sampled leaf), which in most cases, are the greatest constraints of other diagnostic approaches (Beaufils, 1971, 1973; Sumner, 1977a,b,c; Walworth and Sumner, 1987). Application of the DRIS is limited mainly by the lack of sufficient data on nutrient concentrations (Beaufils, 1973; Weetman and Wells, 1990) and also by the complexity of the methodology which has discouraged its use (Jones, 1981). Hockman and Allen (1990) state that the greatest advantage of DRIS as a diagnostic technique is the ability of this system to incorporate nutrient balance, one of the most important requirements for accurate fertiliser recommendations. The DRIS approach seems best suited as a basis on which to develop site-specific fertiliser recommendations as many factors, including non-foliar variables and soil-based norms, can be included in the diagnosis (Herbert and Schönau, 1989; Herbert, 1996).

2.2.2.5 The deviation from optimum percentage (DOP) index

The deviation from optimum percentage (DOP) index is similar to the DRIS approach, where the nutrient limitation is ordered in terms of requirement, and negative or positive indices indicate nutrient deficiencies or excesses, respectively (Montañés *et al*., 1993). The DOP index is defined as the percentage deviation of a nutrient element from the optimum concentration, taken as the reference value (Montañés *et al*., 1993). Reliable reference data are needed to interpret foliar analyses and correctly diagnose the nutritional status (Montañés *et al*., 1993). The sum of the DOP index values is analogous to the NBI in DRIS (Montañés *et al*., 1993). According to Montañés *et al*. (1993), one of the advantages of the DOP index is that this method provides a definitive indication of the nutritional status of a particular element, in comparison to the DRIS indices which may vary when the composition of other elements change. In addition, the DOP indices can be converted back to the original nutrient concentrations provided the reference value for the nutrient is known (Montañés *et al*., 1993).

This brief review of the various diagnostic techniques illustrates the similarities between the DRIS and DOP index, and the optimum nutrient ratio approach (adopted for use in this study). The optimal foliar target values in this trial were those recommended by Linder (1995) for optimal nutrient status in Norway spruce trees. The principal objective of Chapter 8 was to determine whether these optimal ratios could be fine-tuned to make them specific to *E. grandis*. Limited data exist for optimal foliar concentrations in South African *E. grandis* trees older than one year, and therefore these values would have to be derived from available literature. It was decided that the DRIS approach would be the most appropriate technique by which this could be achieved.

2.3 OVERVIEW

This review of the literature has highlighted the importance of water stress and nutrient deficiencies as the main limitations to plantation growth. An international network of experiments has been established with the aim of demonstrating the potential yield of a forest species by eliminating water and nutrients as growth-limiting factors. Results from these networked nutrient optimisation experiments conducted on *Pinus radiata* in Australia (Linder *et al.*, 1987), *E. globulus* in Portugal (Pereira *et al.*, 1989, 1994), *P. abies* in Sweden (Linder, 1995; Bergh *et al*., 1999), and *P. taeda* in the USA (Albaugh *et al.*, 1998) have shown that the greatest responses occurred where the nutritional status of the trees was optimised under non-limiting soil water availability.

CHAPTER 3

MATERIALS AND METHODS

3.1 SITE LOCATION AND DESCRIPTION

The trial is located on the Came farm in the Seven Oaks/New Hanover area of the KwaZulu-Natal Midlands (Lat. 29^{o} 14’ S, long. 30^{o} 33’ E, alt. 1113 m a.s.l.). This study was conducted over a four-year period from the time of planting in March 1999. For the purposes of this PhD study, field data were collected from planting until the final harvest in December 2002. The trial is still on the land, and is scheduled for harvesting in 2007. This site was previously under dryland production of *Eragrostis curvula* pasture and was chosen primarily because of its proximity to a suitable and sustainable water source on Sappi property. A map of the trial location is presented in Figure 3.1.

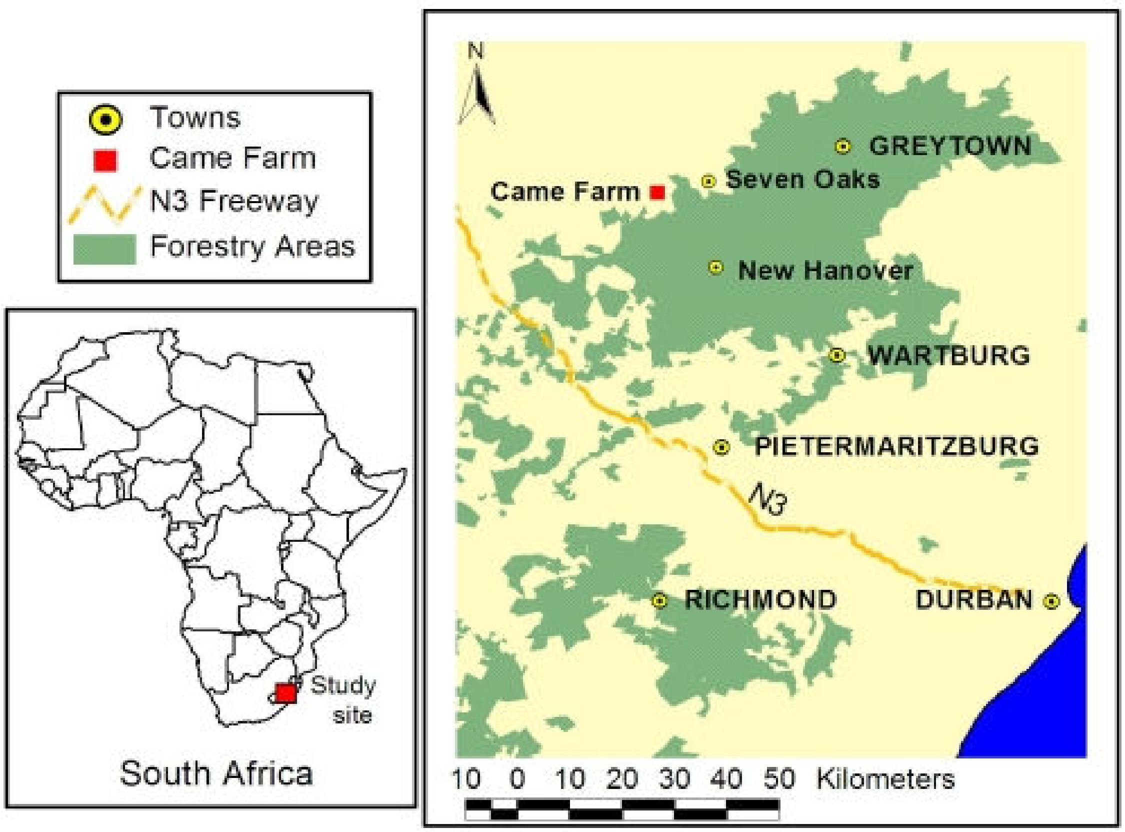

Figure 3.1 Site map showing the trial location and other forestry areas in this region of KwaZulu-Natal, South Africa *(Kindly drawn by Steven Dovey of the ICFR)*.

The site has a mean annual precipitation of 919 mm, with pronounced seasonal rainfall occurring predominantly during the summer months of November to March. The mean annual temperature is 16.6 ^{o}C. The soil is derived from shale parent material and belongs to the Kranskop/Magwa soil form (Soil Classification Working Group, 1991). The physical and chemical properties of the surface soil prior to treatment initiation are presented in Table 3.1.

Table 3.1 Physical and chemical properties of the surface soil (0.0 – 0.4 m) prior to treatment initiation.

Particle size distribution[a]	38% clay 48% silt 14% sand
$pH_{(KCl)}$[b]	4.0
Available P[c]	22.0 mg kg^{-1}
Organic carbon[d]	4.69%
Total N[e]	0.36%

[a] Pipette method

[b] 1:2.5 suspension of soil in extractant

[c] Bray-2

[d] Walkley-Black

[e] Kjeldahl digestion

[a] Handbook of Standard Soil Testing Methods for Advisory Purposes (1990)

[b-e] Heffernan (1985); Kalra and Maynard (1991); Nicholson (1984)

The experiment was planted on a highly weathered acid mineral soil ($pH_{(KCl)}$ 4.0) with a silty clay loam texture, which allows excellent retention of water and nutrients (White, 1979). The soil is relatively fertile, with a high available P concentration of 22.0 mg kg^{-1} (Bray-2) and relatively high values of organic carbon and total N (4.69 and 0.36%, respectively) (Table 3.1). The soil is well-drained and has an average depth of approximately 0.78 m across the experimental area.

3.2 PRE-PLANT TILLAGE OPERATIONS AND VEGETATION CONTROL

Vegetation control consisted of a combination of manual weed removal and herbicide application. The site was sprayed with Roundup (glyphosate, 4 ℓ ha^{-1}) in November 1998 to kill off the *Eragrostis curvula* pasture. The land was ripped to a depth of 0.4 m, rotavated with a 1.2 m rotavator, and pitted with standard 0.25 x 0.50 m pits in the riplines. Two-month-old *Eucalyptus grandis* Hill ex Maiden seedlings were planted in March 1999. All trees were manually ring cleaned and weed growth was slashed in April and October 1999. The site was re-sprayed with Roundup (4 ℓ ha^{-1}) in October 1999.

3.3 EXPERIMENTAL DESIGN AND IMPOSED TREATMENTS

The experiment covered a total area of 6.5 ha and consisted of 16 plots, each measuring 54 x 75 m. The *E. grandis* seedlings were planted at a 2.0 x 3.0 m spacing, producing an initial stocking of 1667 stems per ha. Each replicate plot contained 675 seedlings, and measurements were initially conducted on the 30 centrally-located trees. From February 2002, the number of measured trees was increased to 80 trees per plot (see Section 3.5.7). At least three blanking procedures took place within the internal measurement plots, and all blanked trees were eliminated from further analyses.

The experimental design consisted of four treatments: control, irrigation, fertilisation, and irrigation and fertilisation combined (C, I, F and IF, respectively), initially with four replicates per treatment, arranged in four blocks. These treatments aimed to eliminate both water (I and IF), and nutrients (F and IF) as growth-limiting factors. Due to equipment constraints, the trial was laid out as a split-plot, complete block design, with irrigation as the whole plot and fertilisation as the sub-plot factor. The fertilisation treatment was systematically alternated within the whole plots in each of the four blocks.

3.3.1 Irrigation

The irrigation treatment was initiated in April 1999. Water was applied on a weekly basis using a drip irrigation system with a dripper line in every tree row. Irrigation was aimed at replacing the amounts lost through evapotranspiration, calculated using the Penman-Monteith equation (Mottram, 2004 *pers. comm.*). A soil water depletion level of 70% of the field capacity was used in the irrigation scheduling. Irrigation events commenced once the soil water depletion level was reached; the irrigation applied brought the soil moisture back to the field capacity level. Field capacity was determined by wetting a selected volume of soil to > 0.50 m deep, covering the soil with plastic sheeting to prevent surface evaporative losses, and allowing it to drain for 48 hours, following which, gravimetric soil samples were collected at 0.15 m intervals (*viz*. 0.15, 0.30 and 0.45 m;

Mottram, 2001 *pers. comm.*). Wilting point was determined using the clay content of the soil and regression equations (see Mottram *et al*., 1981) (Mottram, 2001 *pers comm.*). The available water capacity was calculated as the difference between the field capacity and the wilting point (Table 3.2).

Table 3.2 Selected soil water characteristics to a depth of 0.45 m prior to treatment initiation.

Soil depth (m)	**Field capacity** (mm m^{-1})	**Wilting point** (mm m^{-1})	**Available water capacity** (mm m^{-1})
0.15 m	458	283	175
0.30 m	501	321	180
0.45 m	535	334	201

The mean available soil water content to a depth of 0.45 m across the trial area was determined as 83 mm, calculated as the product of the soil depth and the available water capacity. The irrigation water was not chemically analysed, but it was assumed that the quality of the water was constant over time and did not differ between any of the irrigated plots. Monthly rainfall and irrigation amounts received by the *E. grandis* trees are presented in Table 3.3.

Table 3.3 Monthly water amounts (mm) received by *E. grandis* trees from rainfall and irrigation over the period March 1999 to December 2002. Irrigation data were recorded from July 1999 onwards. Irrigation was terminated at the end of October 2002.

	Jan	**Feb**	**March**	**April**	**May**	**June**	**July**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**	**Total**
							1999						
Rain			90	11	6	0	2	28	15	89	34	109	**383**
Irrig.							15	66	66	63	36	12	**258**
							2000						
Rain	88	79	103	50	87	4	0	0	67	67	126	172	**841**
Irrig.	36	63	48	34	24	10	23	24	17	15	0	0	**294**
							2001						
Rain	75	78	47	149	13	0	0	0	78	163	117	105	**825**
Irrig.	3	3	14	19	24	42	54	15	0	38	5	0	**216**
							2002						
Rain	121	66	56	49	6	12	127	81	40	32	60	61	**710**
Irrig.	25	6	15	23	22	0	0	20	48	24	0	0	**181**

3.3.2 Fertilisation

Nutrients were applied to the fertilised treatments according to the results of routine foliar analyses (see Section 3.4.2.2). Fertiliser application was aimed at maintaining foliar elements at specified target levels: an optimal N status was defined, and the proportional percentage of elements relative to N were set at values of 10 (P), 35 (K), 2.5 (Ca), 4 (Mg), 0.05 (Mn), 0.2 (Fe), 0.05 (zinc, Zn), 0.02 (copper, Cu), and 0.05 (boron, B), recommended by Linder (1995). In the early stages of the study, up to two years of age, an optimal N concentration of 28 mg g^{-1} was defined, recommended by Herbert (1996). This value was derived essentially from one-year-old trees (Herbert, 1996). From age two years onwards, the N concentration was set at a target level of 23 mg g^{-1}. As limited data exists for optimal foliar concentrations in South African *E. grandis* trees older than one year, this value was acquired from the available literature from both national and international studies. This target level was based on adequate nutrient ranges and tabulated data from *E. grandis* stands with high productivity, and was assumed optimal (Schönau and Herbert, 1983; Herbert, 1990; Bellote and Silva, 2000; Silveira *et al*., 2000).

Linder (1995) used diagnostic foliar analysis to establish and maintain optimal nutrient status in Norway spruce trees. Target values were set for the foliar nutrient concentrations of each element, based on results obtained from laboratory studies and long-term forest nutrition experiments, in which plant nutrient requirements were established. According to foliar analysis and predicted growth response, the quantities of nutrients needed to be added were estimated in relation to the target value (Linder, 1995). This technique, although applied to Norway spruce, is applicable to other higher plants, as all leaves have a similar inherent function and use an identical array of nutrients in the synthesis of organic matter and other physiological processes (Ericsson *et al*., 1992; Negi and Sharma, 1996). Whilst these nutrient ratios are probably applicable to *E. grandis* trees, it is desirable to use values that have been developed specifically for this species. From age two years, the foliar concentrations of P and K relative to N were set at values of 7.5 and 33.0, respectively, based on recommendations by Schönau and Herbert (1983). As the nutrient ratios recommended by Linder (1995) produce “safe” optimum foliar levels (Linder, 2001 *pers. comm.*), it was assumed that these revised target levels, which were lower than the initial target values of 10 (P) and 35 (K), would still yield optimum growth.

The quantities of nutrients applied to the fertilised (F and IF) trees are presented in Table 3.4.

Table 3.4 Quantities of nutrients applied to fertilised (F and IF) *E. grandis* trees over the first four years of growth.

Date	Tree age (years)	Nutrient application (kg element ha^{-1}), and sources of fertiliser applied					
		N	**P**	**K**	**Ca**	**Mg**	**B**
		LAN[1]	Single supers[2]	KCl[3]			Solubor[4]
01/07/1999	0.5	17.0	0.0	0.0	1.9	1.5	0.0
05/04/2000	1.3	50.0	0.0	0.0	5.7	4.3	0.0
08/08/2000	1.6	10.0	30.0	30.0	49.7	1.0	2.0
29/05/2001	2.3	29.0	11.0	25.0	21.1	2.6	2.0
24/01/2002	3.0	0.0	22.0	22.0	35.6	0.1	0.0
21/10/2002	3.8	0.0	50.0	0.0	81.0	0.0	0.0
	Total	**106.0**	**113.0**	**77.0**	**195.0**	**9.5**	**4.0**

[1] Limestone ammonium nitrate, 28% N; 3.2% Ca; 2.4% Mg
[2] Single superphosphate, 10.5% P; 17.0% Ca
[3] Potassium chloride, 50% K; 0.3% Mg
[4] A highly soluble B fertiliser derived from sodium borates, 16.5% B

All nutrients were applied as solid fertiliser. The first five fertiliser applications (over the period 01/07/1999 – 24/01/2002) were localised, with fertiliser being applied to the surface around each tree. The final fertilisation event (21/10/2002) consisted of a broadcast application. The objective of fertilising at, or soon after planting, is to supply individual trees with sufficient nutrients to promote root establishment, rather than the effect of a broadcast fertiliser application, which would increase the fertility of the entire site (Herbert, 1985).

3.4 DATA COLLECTION

3.4.1 Meteorological Data

Meteorological data were sourced from long-term climatic data or from nearby weather stations. Daily and monthly temperature, relative humidity and solar radiation data were collected from an automatic weather station situated at a nearby research site in the Seven Oaks district (Lat. 29° 11' S, long. 30° 40' E, alt. 1110 m a.s.l.). The distance from the trial site is 12.5 km and the altitude difference is 3.0 m. Real-time monthly rainfall data were extracted from a raster database (Lynch, 2003) by selecting a rainfall station at a similar altitude and with a long continuous data record that was located closest to the site. The altitude of the selected rainfall station is 1084 m a.s.l., and the distance from the trial site is 4.9 km. Long-term monthly mean solar radiation data were required in Chapter 6, and these were obtained from the 1´ x 1´ latitude by longitude digital database developed by Schulze (1997).

3.4.2 Growth Measurements and Sampling

Data were collected according to the three main focus areas of this study, *viz*. tree-water relations, nutrient dynamics and acquisition, and carbon allocation. The site was characterised in terms of the initial soil physical and chemical properties, soil depth, and nutrient status. Growth data were intensively collected during the early stages of the trial: Measurements of tree height, diameter (at 5.0 cm (groundline diameter, gld) and at 1.3 m (diameter at breast height, DBH)) and canopy volume were conducted on a monthly basis until August 2000 (trees aged 19 months). Sampling intensity was later reduced to bi-monthly measurements until December 2000, after which growth data were collected approximately four times per year. Diameter at breast height measurements and the subsequent calculation of basal area and stem volume commenced in March 2000. The collection of gld and canopy volume data ceased in December 2000.

3.4.2.1 Tree-water relations

Pre-dawn xylem pressure potential was measured four times over the period June 2001 – June 2002 to assess the plant water status in each treatment. Sap flow data were recorded in the irrigated-only (I) treatment using the heat pulse velocity (HPV) technique as a measure of the rate of water use of trees experiencing no significant soil water deficits. A simple canopy conductance model was constructed using inputs of *D* and solar radiation, and was used with the Penman-Monteith equation to predict daily transpiration rates by *E. grandis* trees at a second site.

3.4.2.2 Nutrient dynamics

Routine foliar analysis was conducted to assess the plant nutrient status and response to fertiliser application. Foliar samples were intensively collected during the early stages of the trial, on a monthly basis until January 2000 (trees aged one year). Subsequently, the sampling intensity was reduced, and foliage was analysed approximately three times per year. Initially, foliar samples were obtained by stripping all leaves from six harvested trees per plot, as sufficient foliar material was required for nutrient analysis. From January 2000, approximately 30 of the most recent, fully-developed undamaged leaves were collected at random from the outer branch position from all sides of the top third of the crown of each of six trees per plot. All foliar material was bulked on a per-plot basis, placed in paper bags and packed in cool boxes for transport to the Institute for Commercial Forestry Research (ICFR, Pietermaritzburg, KwaZulu-Natal) laboratory for nutrient analysis using the methods outlined by Nicholson (1984), Heffernan (1985) and Kalra and Maynard (1991). Foliar material was analysed for total N by Kjeldahl digestion and titration. After dry ashing, P concentration was determined spectrophotometrically using the molybdenum blue method and segmented flow autoanalyser. Foliar samples were also analysed for K and Na (flame emission spectroscopy), Ca, Mg, Mn, Cu, Fe, Zn (atomic absorption spectroscopy), and B (segmented flow autoanalyser).

3.4.2.3 Carbon allocation

Carbon allocation was assessed in terms of the biomass produced and the subsequent partitioning between component parts of the trees. Destructive harvests were carried out to obtain biomass estimates of trees aged approximately two, three, and four years. Sample trees were selected to represent the range in DBH at the time of harvesting. The various biomass components of the sample trees were regressed against DBH and tree height, and regression equations explaining the largest proportion of the variation were used to estimate biomass values for individual trees in each of the treatments. The individual tree biomass data were summed to a plot level and scaled to a per ha value. Leaf areas were measured and used for the calculation of specific leaf area (leaf area per unit dry leaf mass) and hence L. These values and estimates of above-ground biomass and partitioning were used to validate the 3-PG model. Sampling at four years also provided estimates of biomass pools contained in the soil, forest floor and below-ground components. The N and P contents contained in these pools and in the above-ground fractions were quantified. The specific methodology pertaining to each section, and the associated statistical analyses are presented in greater detail in the relevant chapters.

3.5 OPERATIONAL AND RESEARCH CONSTRAINTS

This research was hampered by a number of constraints including poor seedling quality, inadequate vegetation control, insufficient irrigation, late fertiliser application, damage from animals, and vandalism and theft of equipment. In this trial, neither water nor nutrients were completely eliminated as growth-limiting factors and the potential yield of *E. grandis* growing under the given climatic conditions could not be demonstrated. Consequently, the experiment served to provide comparisons between the different treatments, rather than demonstrate maximum growth and production under conditions of optimised water and nutrient availability.

There are many risks associated with any experiment of this nature, particularly with intensive management, and when carried out on a long-term basis. In South Africa, these types of risks arise most frequently from extreme weather conditions such as drought, fire and snow, and damage caused by hail and windstorms. The growth in this trial was constrained, mainly as a result of poor establishment and management practices, and also from the effects of two windstorms at the site. In addition, frequent vandalism and theft of equipment served as a hindrance to data collection. Each of these constraints is discussed in turn.

3.5.1 Experimental Design

Due to equipment constraints, the trial was laid out as a split-plot complete block design with irrigation as the whole plot and fertilisation as the sub-plot factor. As a result, the irrigation component of the trial was not replicated. Consequently, contrasts between irrigated plots and those plots that did not receive additional water would be confounded with the difference between these two blocks, as units of land. For example, if the soil in block A was more fertile and resulted in better growth than in block B, this would add a component to the contrast between ‘irrigated’ and ‘non-irrigated’, and there would be no information which would allow separation of the ‘soil’ effect from the ‘irrigation’ effect. If available data or other independent information revealed that there was no difference between the two blocks, then it would be valid to treat the ‘irrigated’ versus ‘non-irrigated’ contrast as a reflection of the effect of irrigation (Harding, 2004 *pers. comm.*). The use of this approach and appropriate statistical techniques (see Chapter 5) allowed for adequate data analysis and interpretation.

3.5.2 Seedling Quality

The origin of the planting material was open-pollinated orchard seed of mixed provenance background. The seed batch was supposedly improved genetic material, but there was evidence of a poor and variable seed stock, with the appearance of many 'runt' trees. These 'runts' had much smaller leaves and very poor, bushy growth forms compared to the remaining trees. This was attributed to non-synchronous flowering in the seed orchard.

3.5.3 Vegetation Control

The pre-plant tillage was not successful in that the previous plant material was not killed off, resulting in regrowth of both *Eragrostis curvula* and numerous weeds. The weeds grew vigorously throughout 1999, which caused a marked competition in the establishment of the seedlings, and thereby negatively impacted seedling survival and growth. Fertilisation can stimulate the growth of competing vegetation, resulting in a reduction in the growth response of plantation trees through competition for site resources such as light, water or nutrients (Gonçalves *et al*., 1997).

3.5.4 Irrigation

Ideally, eucalypt seedlings should be planted in November to coincide with the first summer rainfall period. There was a delay in the planting of the trial until March, due to extreme climatic conditions and a delay in the installation of the irrigation system. Weed growth was manually removed by slashing in April and October 1999. Unsupervised labour resulted in the irrigation dripper lines being repeatedly cut. In addition, a burst pipe in the pumphouse caused severe electrical breakdowns and subsequent pump failure from end May to mid-August 2002. Consequently, irrigated (I and IF) trees only received rain water during this winter period.

3.5.5 Fertilisation

Fertiliser was not applied at planting, or soon thereafter, which is the standard forestry practice in South Africa. A full fertiliser dosage as soon as possible (within five weeks) after planting is recommended (ICFR, 2000). The first nutrient application only occurred on 01/07/1999 (trees aged six months) due to difficulties in ordering and delivery of the fertiliser. Optimum responses to fertiliser application will only be attained if sound nursery stock is used, the fertiliser is correctly positioned, and weeds are properly controlled (Herbert, 1990) for nine to twelve months after application (Herbert, 1985).

3.5.6 Damage from Animals

Local farmers from the surrounding rural areas allowed cattle and sheep to enter the trial area, which resulted in seedlings being damaged and the dripper lines being moved away from their position alongside the trees. Only after numerous requests was this situation rectified. Furthermore, there was extensive browsing by small antelope in some areas of the trial.

3.5.7 Effect of Windstorms

Many trees were extensively damaged by the effects of two very severe windstorms which occurred in the plantation during October and November 2001. After conducting a complete site inventory in February 2002, it was decided to eliminate one replicate of each treatment due to the extent of the damage in these plots. Measurements were initially conducted on 30 centrally-located trees; the number of measured trees was increased to 80 trees per plot to account for the variability following the windstorms. All results presented from February 2002 onwards are the means of three replicates per treatment. At the final measurement (age four years), the stocking in the C, I, F and IF treatments was 1250, 1181, 1261 and 1194 stems per ha, respectively.

3.5.8 Vandalism and Theft of Equipment

An automatic weather station was erected on a neighbouring farm within 5 km of the trial site. The weather station was set up shortly after the trial was established, and recorded incoming solar radiation, temperature, relative humidity, wind speed and direction, and rainfall. Unfortunately this was vandalised on several occasions resulting in loss of expensive equipment and data. Consequently, these data had to be sourced from elsewhere (see Section 3.4 above). Sap flow data were measured using the HPV technique; these results are presented in Chapter 7. Initially, two sample trees were selected from one replicate plot from each of the control, and irrigated-only treatments (*n* = 4 in total). The first phase of sampling spanned the period from mid-August to mid-November 2001. A second phase of sampling was initiated on two further trees in each plot, but was prematurely terminated in February 2002 following the theft of the HPV equipment. The sap flow data record was less extensive than originally planned, due to theft of equipment and frequent data logger malfunction believed to result from considerable dampness at the trial site, as well as aging electronic components (Dye and Xaba, 2002).

Given these constraints, it is clear that this research was hindered, and maximum growth at this site could not be achieved, even with the combined application of water and nutrients (IF treatment).

CHAPTER 4

INFLUENCE OF IRRIGATION AND FERTILISATION ON EARLY GROWTH OF *EUCALYPTUS GRANDIS*[1]

4.1 INTRODUCTION

Available moisture and nutrients strongly influence plantation forest growth, as these are the most common factors which limit productivity (Brown *et al.*, 1997). Generally, nutrient limitations are overridden by climatic restrictions, as even trees in a very fertile soil will not grow under limited water supply or when temperature is unfavourable (Landsberg and Waring, 1997). According to Schönau and Herbert (1989), the main factors influencing stand development of *Eucalyptus* plantations are soil moisture, nutrients, organic matter, effective rooting depth, quality of seed and nursery material, site preparation and vegetation control. Of these, soil moisture and nutrients are regarded as being the most important (Schönau and Herbert, 1989).

Due to the importance of *E. grandis* in South Africa, together with the anticipated increase in timber demand and the limited availability of land for afforestation, suitable management regimes must be implemented to ensure these plantations generate high levels of productivity on a sustainable basis. Utilising more land for wood production would increase supply (Brown and Hillis, 1984), but this expansion may be limited by many restrictions, such as permits, availability of suitable land and water issues (Dye, 1999). Improving the productivity of new and re-established plantations can partially compensate for the deficit in new afforestation (Schönau, 1983). Fertiliser application is one of the most cost-effective methods of economically improving and maintaining the productivity of commercial plantations (Schönau, 1983; Herbert and Schönau, 1989).

The development of research on fertiliser applied to trees at planting in southern Africa has been extensively reviewed by Schönau (1983), Schönau and Herbert (1989) and Herbert and Schönau (1989, 1990). These studies indicated that *E. grandis* responded mainly to N and P applied at establishment, and that the proportions of these elements

[1] Published in *Discovery and Innovation* 15: 213 – 220 (2003).

must be finely balanced. Responses to fertiliser have included rapid colonisation of the soil by the roots, improved survival, rapid canopy closure and suppression of weeds, a more homogeneous stand and increased yields at harvesting (Herbert, 1985).

As extreme nutritional disorders are uncommon, fertiliser is applied to optimise conditions for growth (Herbert, 1996). Nutrient optimisation involves the repeated additions of nutrient elements relative to N. Many long-term studies have aimed to determine the effects of 'near-optimal' water and nutrient availability on the growth of trees, e.g. *P. radiata* in Australia (Linder *et al.*, 1987), *E. globulus* in Portugal (Pereira *et al.*, 1989, 1992), *P. taeda* in the USA (Albaugh *et al.*, 1998) and *P. abies* in Sweden (Bergh *et al.*, 1999). In all of these experiments, the greatest volume yields and best growth in terms of height and diameter values were obtained from trees where the availability of water and nutrients was optimised.

A similar type of field trial was set up near New Hanover, KwaZulu-Natal, South Africa. This study aimed to determine the influence of irrigation and fertiliser application on the growth of *E. grandis*. Two hypotheses were formulated: firstly, as a result of climatic limitations outweighing nutrient deficiencies, growth would be high on the irrigated treatment, but because of a synergistic effect, maximum growth would be attained on the irrigated and fertilised treatment, and secondly, by diagnostic foliar analyses, the proportions of elements relative to N could be manipulated and improved. The purpose of acquiring these results was to demonstrate potential forest yields by adjusting nutrient and water supply to uptake requirements.

4.2 MATERIALS AND METHODS

4.2.1 Site Description and Experimental Design

A description of the site and an outline of the experimental design are presented in Sections 3.1 and 3.3, respectively.

4.2.2 Treatments

The treatments are described in greater detail in Sections 3.3.1 and 3.3.2. The fertilised (F and IF) trees received 67 kg N ha^{-1} over the first 17 months of growth, applied in the form of LAN (Table 3.4).

4.2.3 Growth Measurements

Tree height, diameter and canopy volume were measured monthly from May 1999 (trees aged four months). Diameter was measured both at ground line and at 1.3 m. The latter measurements commenced in March 2000, when the average tree height of the internal plots measured approximately 2.7 m across all treatments. Canopy volume was calculated using the formula of a spherical cylinder:

Volume = $\surd r^2h$, where $\surd$= 3.14, r^2 = (canopy radius)^2 and h = canopy height.

Canopy height was measured from the lowest live branch on the stem to the shoot apex. Canopy radius was calculated from the canopy diameter; the distance measured from the centre of the stem to the two furthest leaves on each side of the stem.

4.2.4 Foliar Nutrient Concentrations

The methodology pertaining to foliar sampling and subsequent nutrient analysis is outlined in Section 3.4.2.2.

4.2.5 Statistical Analyses

All data were subjected to a 2 x 2 factorial analysis of variance (ANOVA), using the Statistica (Statsoft, 2000) package to test for any significant ($p \leq 0.05$) treatment effects. Data were checked with residual plots for the assumptions of normality and constant variance.

4.3 RESULTS

4.3.1 Stem Height

The cumulative height growth of *E. grandis* until 17 months of age is depicted in Figure 4.1. Stem heights at this age were 3.6 (C), 3.1 (I), 3.6 (F), and 3.8 m (IF). Treatment effects were not significant.

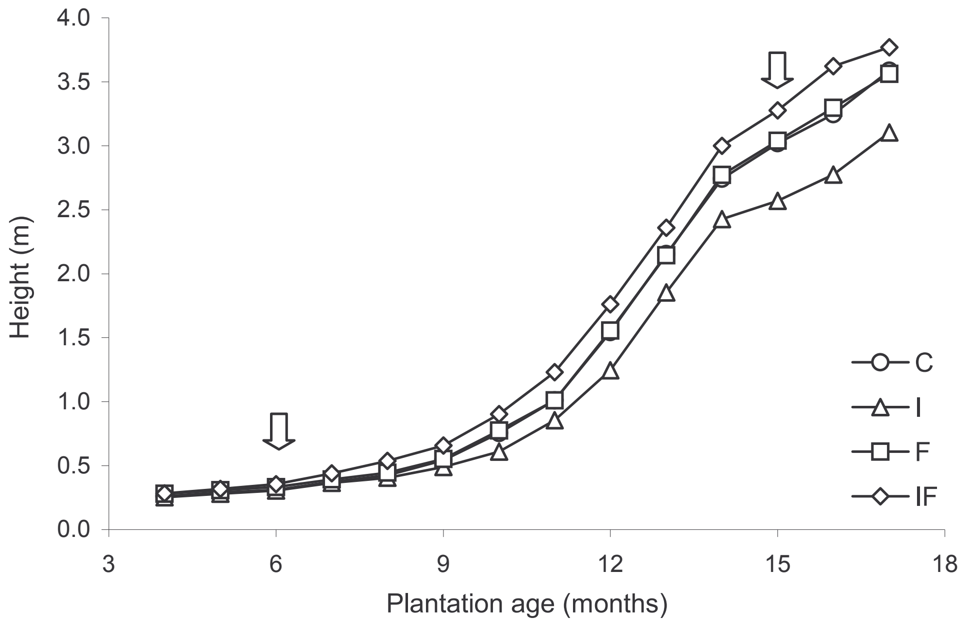

Figure 4.1 Cumulative height growth of *E. grandis* under various treatment regimes, C = control, I = irrigation, F = fertilisation and IF = irrigation and fertilisation. Values presented represent the mean height in each treatment, which is the average of the four blocks. Arrows indicate fertilisation events.

4.3.2 Stem Diameter

Stem diameter at ground line increased continuously until 17 months of age, where respective values of 6.5, 6.0, 6.4, and 7.4 cm for the C, I, F and IF treatments were measured (Figure 4.2).

The DBH of 17-month-old *E. grandis* trees was 3.4, 3.6, 3.5, and 4.5 cm for the C, I, F, and IF treatments, respectively (Figure 4.3). No significant treatment effects were observed in either the gld or the DBH values.

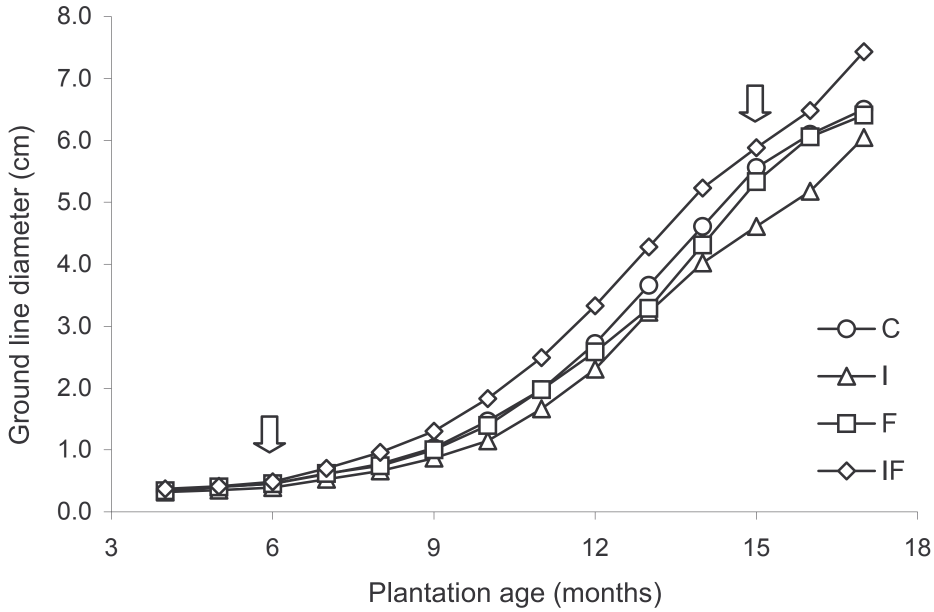

Figure 4.2 Accumulative stem diameter at ground line of *E. grandis* subjected to different treatments. Values presented represent the mean diameter in each treatment, which is the average of the four blocks. Arrows and abbreviations as for Figure 4.1.

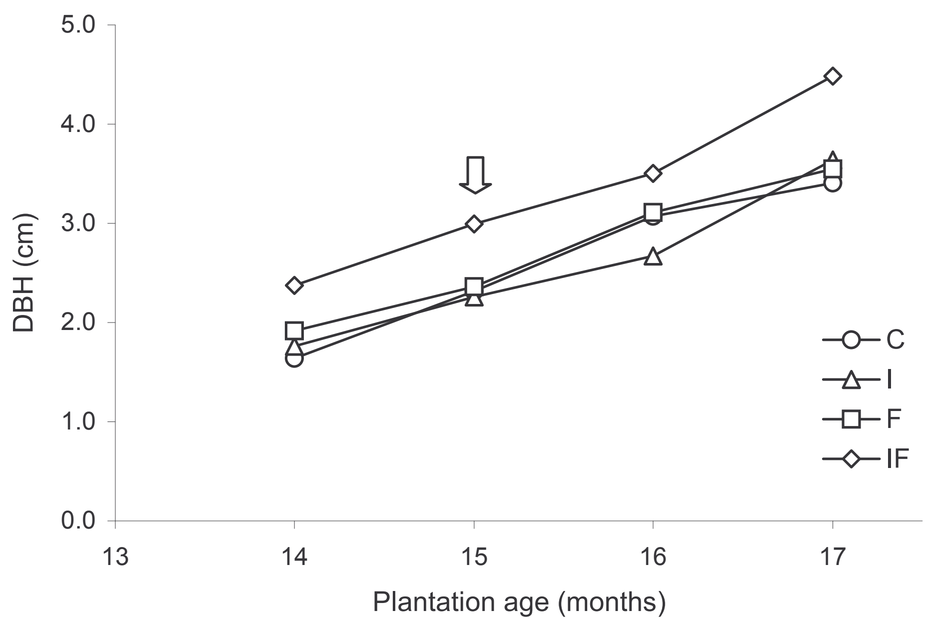

Figure 4.3 Increase in *E. grandis* DBH, aged 14 to 17 months. Values presented represent the mean DBH in each treatment, which is the average of the four blocks. Arrows and abbreviations as for Figure 4.1.

4.3.3 Canopy Volume

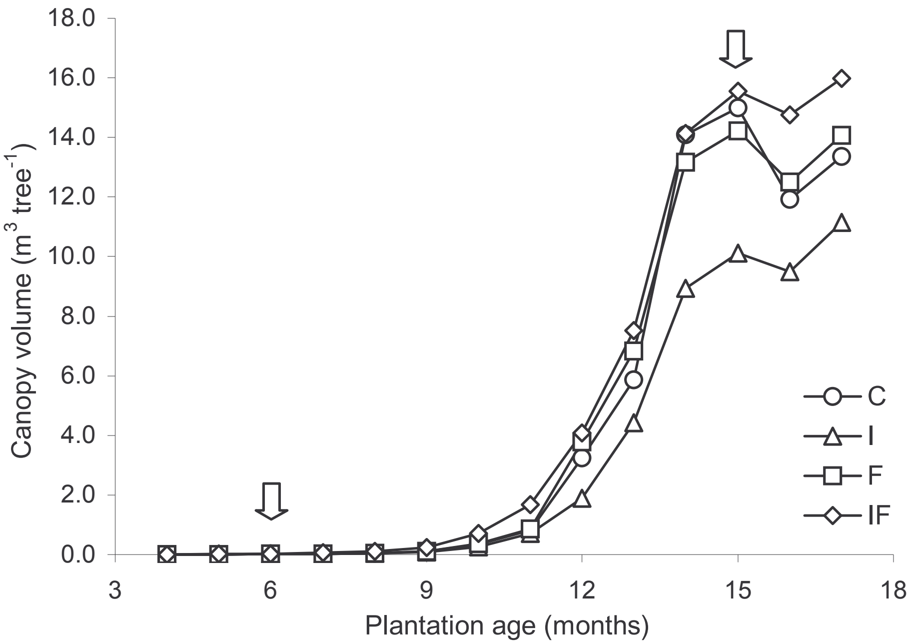

Figure 4.4 Cumulative canopy expansion of *E. grandis* subjected to various treatments. Values presented represent the mean volume in each treatment, which is the average of the four blocks. Arrows and abbreviations as for Figure 4.1.

There was a steady increase in the canopy volume in all treatments until 15 months of age (Figure 4.4). At this time, values of 15.0, 10.1, 14.2, and 15.6 m^3 $tree^{-1}$ were measured for the C, I, F, and IF treatments, respectively. A decrease in the canopy volume across all treatments occurred over the period 15 to 16 months: 15.0 – 11.9 (C), 10.1 – 9.5 (I), 14.2 – 12.5 (F), and 15.6 – 14.8 m^3 $tree^{-1}$ (IF), but were observed to increase again thereafter. Treatment effects were not significant.

4.3.4 Foliar Nutrient Concentrations

The foliar nutrient concentrations and their ratios of one-year-old trees, presented in Table 4.1, were within the encountered ranges documented by Herbert (1996).

Table 4.1 Foliar nutrient concentrations and some of their ratios (mean (standard deviation)) for one-year-old *E. grandis*, together with their optimum values and encountered ranges in South Africa. The different treatments are control (C), irrigation (I), fertilisation (F), and irrigation and fertilisation (IF).

Foliar Nutrient or Ratio	Units	KwaZulu-Natal Study				Comparative values (Herbert, 1996)		
		C	I	F	IF	Opt	Min	Max
N	%	3.45 (0.14)	3.51 (0.13)	3.45 (0.13)	3.42 (0.12)	2.8	1.25	3.35
P	%	0.20 (0.01)	0.21 (0.01)	0.19 (0.03)	0.21 (0.01)	0.15	0.10	0.35
K	%	0.99 (0.09)	0.78 (0.11)	0.85 (0.06)	0.90 (0.18)	0.75	0.36	1.19
Ca	%	1.01 (0.11)	0.96 (0.06)	1.06 (0.08)	0.99 (0.14)	>1.0	0.56	1.82
Mg	%	0.22 (0.02)	0.24 (0.02)	0.23 (0.02)	0.23 (0.02)	0.35	0.21	0.62
Na	%	0.25 (0.00)	0.29 (0.04)	0.23 (0.05)	0.28 (0.09)	0.32	0.11	0.46
Mn	ppm	807.25 (150.07)	556.25 (106.29)	699.50 (91.90)	591.00 (40.98)	600	129	6005
Fe	ppm	78.00 (9.70)	71.50 (4.43)	71.00 (8.83)	71.75 (1.26)	110	52	1021
Zn	ppm	35.25 (7.14)	35.25 (3.40)	37.25 (10.72)	33.75 (3.69)	18	8	32
Cu	ppm	12.75 (1.71)	13.50 (1.91)	11.00 (0.82)	12.25 (0.96)	12	2	26
B	ppm	21.50 (3.00)	20.25 (1.71)	22.25 (2.06)	19.00 (1.41)	32	15	47
N:P		17.56 (1.75)	16.98 (1.67)	18.66 (2.57)	16.11 (0.79)	18	3.0	28.6
N:K		3.51 (0.38)	4.58 (0.60)	4.09 (0.30)	3.91 (0.67)	3.5	1.0	5.4
P:K		0.20 (0.03)	0.27 (0.05)	0.22 (0.03)	0.24 (0.05)	0.2	0.093	0.620
Ca:Mg		4.71 (0.71)	3.95 (0.21)	4.56 (0.08)	4.40 (0.32)	>3.3	1.24	7.28

The Mn concentration in the I treatment was significantly lower (p = 0.005) than that measured in the control. The N:P, N:K, P:K and Ca:Mg ratios in all treatments were found to approach the optimum. In comparison with Linder (1995), however, the P and K concentrations indicated that these nutrients were in limited supply. This author defines an optimal N status in the foliage, and then defines target values for each nutrient element relative to N (Table 4.2).

Table 4.2 Foliar nutrient concentrations and ratios of one-year-old *E. grandis*, compared to target values used as optimal in one-year-old foliage of Norway spruce (Linder, 1995). Abbreviations as for Table 4.1.

Nutrient	Target	C	I	F	IF
N (mg g^{-1})	**[28]**	34.5	35.1	34.5	34.2
P (% of N)	**10**	5.7	5.9	5.4	6.2
K (% of N)	**35**	28.7	22.1	24.5	26.2
Ca (% of N)	**2.5**	29.1	27.2	30.8	29.0
Mg (% of N)	**4**	6.2	6.9	6.7	6.6
Mn (% of N)	**0.05**	2.34	1.59	2.03	1.73
Fe (% of N)	**0.2**	0.23	0.20	0.21	0.21
Zn (% of N)	**0.05**	0.10	0.10	0.11	0.10
Cu (% of N)	**0.02**	0.04	0.04	0.03	0.04
B (% of N)	**0.05**	0.06	0.06	0.06	0.06

The N concentration in all treatments in the KwaZulu-Natal trial was greater than the target value of 28 mg g^{-1} (Table 4.2). The P and K concentrations were interpreted as limiting, as the levels of these elements relative to N were lower than the target values of 10 and 35, respectively. The other nutrients were considered as being in adequate supply, as these ratios exceeded the target levels recommended by Linder (1995).

4.4 DISCUSSION AND CONCLUSION

In an optimisation study on *E. globulus* in Portugal, the height of one-year-old trees measured 2.1, 3.1, 2.6, and 3.5 m for the C, I, F, and IF treatments, respectively (Pereira *et al.*, 1989), compared to the notably lower values of 1.5, 1.3, 1.6, and 1.8 m in this trial. In 14-month-old *E. globulus* trees in Australia, mean heights across three sites ranged from 1.1 – 2.1 m in the control, and from 1.4 – 2.5 m in the fertilised treatment (Judd *et al.*, 1996b). In the current trial, similar aged *E. grandis* trees were taller, with heights of 2.7, and 2.8 m in the control and F treatment, respectively.

In a study assessing the effects of nutrient applications made to *E. grandis* at planting, gld measured in one-year-old control plots was 3.2, compared to 3.1 cm in plots fertilised with N (Carlson *et al.*, 1998). In the KwaZulu-Natal trial, one-year-old C and F trees had gld values of 2.7 and 2.6 cm, respectively. The DBH of 14-month-old *E. globulus* trees in Portugal was 2.0, 3.3, 2.7, and 4.0 cm for C, I, F, and IF, respectively (Pereira *et al.*, 1989). In similar aged *E. grandis* trees in this trial, the DBH values were substantially lower, and measured 1.6 (C), 1.8 (I), 1.9 (F) and 2.4 cm (IF).

The decrease in canopy volume resulted from a large number of trees dropping their lower branches. This phenomenon occurred at random throughout all the treatments, but was observed mainly in the taller trees. Dropping of branches was observed by Herbert (1999 *pers. comm.*) in previous experiments with *E. grandis* during spates of rapid growth. Boron and Cu, important components of branching and lignification, could not be correlated with this phenomenon.

Herbert (1996) stated that a decrease in nutrient concentration does not necessarily result in poorer growth, just as an increase in nutrient uptake does not always signify better growth. Rather, an overall balance of nutrients, i.e. where nutrient ratios approach their optima, results in the best growth. Foliar analyses indicated a limitation of P and K when compared to the target values of Linder (1995). It was anticipated that the nutrient status of the trees could be further improved with the application of fertiliser following these diagnoses.

The height and diameter of the *E. grandis* trees were found to lie within the range quoted for comparable studies. In some instances, however, these values were considerably lower than those cited in the literature. The many problems experienced at the site may have contributed to the poor performance of the trees thus far. Fertiliser was applied late, and heavy trampling from cows and browsing by small antelope caused extensive damage to some areas. The presence of weeds created a problem throughout 1999, causing a marked competition in the establishment of the seedlings. If the maximum benefit from fertilising is to be reached, weed control should be sustained for nine to twelve months following fertilisation, as *Eucalyptus* trees may show little or no response if post-fertiliser weeding is not effectively carried out (Herbert, 1985).

It was hypothesised that as a result of climatic limitations outweighing nutrient deficiencies, growth would be high on the irrigated treatment, but because of a synergistic effect, maximum growth would be attained by trees that were both irrigated and fertilised. Maximum height, diameter (at ground line and at breast height), and canopy volume growth was attained in the IF treatment. The I treatment, however, exhibited very poor growth in comparison. As the foliar analyses did not reveal any major nutritional limitations compared to the other treatments, this may be attributed to a greater disturbance from animals, or to a higher presence of weeds.

Optimum responses to fertiliser will only be attained if healthy nursery material is used, fertiliser is correctly positioned and weeds are properly controlled (Herbert, 1996). If this has been ensured, the annual increase as a response to fertilising may not only be maintained until clear-felling, but may increase over time (Herbert, 1985). Despite the early setbacks in the trial, it was envisaged that if the foliar nutrient concentrations (particularly P and K) relative to N could reach, and be maintained at their optima, the trees would continue to grow at a rapid rate under conditions of increased water and nutrient availability.

The data presented in Chapter 4 indicate that at this stage of stand development, the greatest growth occurred in response to an increased availability of both water and nutrients (IF treatment). The poor growth observed in the I treatment may have resulted from intense weed competition or severe damage from animals. Fertilised (F and IF) treatments received applications of P and K following the diagnosis that these elements were potentially limiting when compared to the target values suggested by Linder (1995). The first objective and key question were addressed by continued monitoring of foliar nutrient concentrations and growth responses. These measurements were conducted to determine whether the addition of P and K improved the nutrient status of the fertilised trees, and to assess the relative importance of water and nutrition in controlling the growth of *E. grandis* at this site, and how this may change over time. Water availability and mineral nutrition influence the dry matter distribution between roots and shoots. Increased availability of these growth resources are reported to reduce below-ground biomass allocation, resulting in more carbohydrates for stem growth, leading to an increase in wood production. The effects of irrigation and fertilisation on above- and below-ground biomass partitioning were investigated at four years of age, and the N and P pools in these biomass fractions were quantified. These results are presented in Chapter 5.

CHAPTER 5

BIOMASS AND N AND P POOLS IN ABOVE- AND BELOW-GROUND COMPONENTS OF AN IRRIGATED AND FERTILISED *EUCALYPTUS GRANDIS* STAND[2]

5.1 INTRODUCTION

Forest productivity can be increased by intensive site preparation, genetic improvement, irrigation, fertilisation and vegetation control (Wise and Pitman, 1981). The rapid growth resulting from intensive silviculture, together with high nutrient uptake over short rotations leads to a greater potential for nutrient loss during timber harvesting (Attiwill and Leeper, 1987; Herbert, 1992; Ericsson, 1994a; Judd, 1996; Santana *et al.,* 2000), which may cause possible problems for sustainable productivity (Hunter, 2001). Nitrogen and P are the two elements most frequently limiting to forest growth (Pritchett, 1979; Grove *et al.,* 1996; Fölster and Khanna, 1997). Concern surrounding long-term sustainability of plantation productivity with respect to these potentially limiting elements has been highlighted in many studies, and nutrient budgets have been constructed, or N and P pools presented for *Eucalyptus* stands (e.g. Herbert and Robertson (1991), Judd (1996), Santana *et al.* (2000), du Toit and Scholes (2002) and du Toit (2003)). Due to the importance of *E. grandis* in South Africa, these plantations need to be grown in a sustainable way. As highlighted by Herbert (2003), the impacts of high-yielding short rotations on sites in this country are not well documented or understood. As such, there is a need to provide points of reference regarding nutritional budgets and estimates of the potential impacts of harvesting on site resources for the local timber industry.

Biomass and nutrient pools of an *E. grandis* stand subjected to intensive silvicultural treatments were estimated in this study to provide a mid-rotation benchmark value as a means to fill this gap in our knowledge. A comparative analysis of above- and below-ground biomass and N and P pools was carried out between the C, I, F and IF treatments of a four-year-old *E. grandis* stand in KwaZulu-Natal, South Africa.

[2] Paper currently undergoing revision as suggested by reviewers for publication in *Australian Forestry*.

Below-ground pools were quantified to understand the potential impact of treatment on above- versus below-ground biomass allocation.

5.2 MATERIALS AND METHODS

5.2.1 Site Description and Experimental Design

A description of the site is given in Section 3.1, and the experimental design and imposed treatments are presented in Section 3.3.

5.2.2 Measurements and Sampling

Sample trees were selected to represent the range in DBH at the time of harvesting, which occurred during the height of summer (December). The representative trees (n = 6 per treatment) were felled at ground level and after measuring the length of the live crown, were separated into stem, foliage, live and dead branches (‘branches’ comprised both twigs and branches) and capsules. Each stem was measured for total length (height) and sample disc sections were cut at 1 m intervals to determine the ratios of stemwood and stembark. Two sets of foliar samples were collected, for i) routine foliar nutrient analysis (see Section 3.4.2.2), and ii) estimation of foliar biomass and nutrient content, based on the collection of leaves from the bulk foliar sample (included damaged and different-aged leaves from all positions in the crown). The average capsule mass was estimated as 32 kg ha^{-1} and was not considered in this study.

Measurements of the root system of *E. grandis* were conducted on each of the smallest, largest and mean sample trees (n = 3 per treatment) harvested for above-ground biomass. The root system was excavated from a 0.5 x 0.5 m area centred around the base of each tree at depth intervals of 0.2 m, to a total depth of 0.6 m, and separated into coarse (> 2.0 mm diameter) and tap roots. Coarse roots arising from neighbouring trees but within the sampling area were also included; roots outside this area were not considered. Fine root (< 2.0 mm diameter) samples were collected by coring with a stainless steel, 1.0 m long corer with a diameter of 84.0 mm to a depth of 0.3 m below the soil surface, based on results from a previous study conducted at this site, which showed that 64 – 82% of fine roots occurred in the 0.0 – 0.3 m horizon (Nkosana, 2002). One soil core was extracted at random from the central sub-plots used for non-destructive measurements, from all the replicate plots, to include spatial variation.

The soil and roots from the cores were separated by mixing the samples with water and passing this mixture over an array of two sieves with mesh sizes of 2.0 mm and 300.0 μm for top and bottom sieves, respectively. After washing, the root samples trapped in the sieves were separated into live and dead by hand, with dead roots recognised by their dark brown colour, wrinkled nature and their fragility when bent with forceps. All above- and below-ground material was weighed for total fresh mass and sub-sampled for dry mass determination and nutrient analysis. Root mass is presented on an ash-free basis to eliminate the effect of soil contamination. Coarse root estimates in the analyses refer to the sum of the tap root and coarse root estimates.

5.2.3 Forest Floor

Forest floor samples from the *E. grandis* stand were collected from three replicate 1 m^2 quadrats randomly located within each sub-plot. Litter was collected to the top of the mineral soil layer. The samples were dried at 70 ^oC until a constant mass, separated into woody and non-woody fractions, and analysed for nutrient concentration. Forest floor mass data are presented on an ash-free basis.

5.2.4 Soil

Three replicates of 10 composite soil samples cored at depths of 0.0 – 0.3 m and 0.3 – 0.6 m were collected at random from each sub-plot for nutrient analysis. Soil nutrient pools for each depth interval were calculated using the formula:

$$\frac{NC}{100} \times BD \times D \times 10\,000$$

where NC = nutrient concentration (%), BD = bulk density (kg m^{-3}) and D = soil depth (m), multiplied by 10 000 to scale up to a per ha value. Mean bulk density for each soil depth was determined from four undisturbed soil core samples per depth. All soil samples were collected from the replicates of the control plots and assumed to be representative of the entire stand. The bulk density of the soil was calculated as 1278 and 1287 kg m^{-3} for the respective soil depths of 0.3 and 0.6 m.

5.2.5 Regression Estimates, Nutrient Contents and Statistical Analyses

After sub-sampling, soil samples were placed in plastic bags and other components in paper bags, and packed in cool boxes for transport to the laboratory. All above- and below-ground tree material was oven-dried at 70 ^{o}C, and the soil samples were dried at 105 ^{o}C. Regression analysis was used to derive estimates for all mass components of individual *E. grandis* trees. The suitability of various combinations of DBH, tree height and length of the live crown was investigated as predictor variables. Data analysis indicated that the power function ($y = ax^b$, where y = mass and x = DBH) provided the best fit for all components, except for dead branch mass, where x = tree height. The data were combined for all *E. grandis* trees where the effect of treatment on regression lines was not significant. After dry mass determination, tree material and forest floor samples were processed for N and P concentration in the ICFR laboratory following the methods outlined in Section 3.4.2.2 for foliar material.

To account for any potential variation in nutrient concentration with tree size, nutrient concentrations of above-ground material were determined on the two smallest and two largest trees harvested per treatment. Estimates of concentrations in roots were made on material from the smallest and largest trees for which the root systems had been excavated for estimates of below-ground material. A single mass-weighted nutrient concentration was calculated and applied to all trees in a treatment. The N and P content of each component was calculated as the product of the mass and nutrient concentration. Mass and nutrient contents calculated for each tree were summed to the plot level and scaled to a per ha value.

Total soil N was determined by Kjeldahl digestion and titration. The total soil P pool was measured as P_2O_5 by XRF analysis. The basic XRF methodology is summarised by Karathanasis and Hajek (1996), while Wilson (2003) outlines the specific procedure used in this study. Soil available P was estimated by extracting with Bray-2 solution (0.03 M NH_4F in 0.1 M HCl) and the P content was determined colourimetrically (molybdenum blue method).

The response variables were initially analysed as a split-plot design, and the whole-plot and sub-plot error terms were compared. In most cases (47 out of 55), the whole-plot error term was either smaller than, or statistically similar to the sub-plot error term, as determined by an *F*-test using a conservative error rate of alpha = 0.25. Because these errors were similar, it was judged that the split-plot design was redundant, and so the trial was analysed as a 2 x 2 factorial with a common error term. The site was very uniform with respect to soil properties (pH, texture, organic carbon content, N and available P concentration). A separate analysis of the main response variables as a one-way, complete block design with four treatments showed that the blocking factor was non-significant (alpha = 0.10) in all cases. Non-significant blocking factors are typical of forestry studies in South Africa. Combining the error terms in the design was in part justified by the site uniformity, and in part because the error terms appeared to be expressing the same random site factors. Minimum replication and the loss of four treatment plots also made estimating a combined error term desirable, and we felt that the combined error term was a better estimate of the true random variability within the study area. All analyses of variance were performed using the General Linear Model procedure (proc. GLM) (SAS, 1999). Data were checked with residual plots for the assumptions of normality and constant variance.

5.3 RESULTS

5.3.1 Stand Characteristics

A summary of the stand characteristics at four years of age is shown in Table 5.1.

Table 5.1 Summary of the stand characteristics at age four years (C = control, I = irrigated, F = fertilised and IF = irrigated and fertilised).

Stand characteristics	C	I	F	IF
DBH (cm)	12.8	13.7	13.2	14.0
Height (m)	14.6	14.8	14.7	15.1
Basal area (m^2 ha^{-1})	17.0	18.6	18.0	19.4
Standing volume (m^3 ha^{-1})	99.9	113.8	106.5	118.6

The same trend was observed in all the growth variables measured, which increased in the order C, F, I and IF (Table 5.1). Irrigation had a more pronounced effect on growth compared to fertilisation, and irrigated (I and IF) trees had DBH, height, basal area (BA) and standing volumes of 13.9 cm, 15.0 m, 19.0 m^2 ha^{-1}, and 116.2 m^3 ha^{-1}, respectively, compared to 13.0 cm, 14.7 m, 17.5 m^2 ha^{-1}, and 103.2 m^3 ha^{-1} in non-irrigated (C and F) trees. These irrigation effects were significant for DBH (p = 0.023), BA (p = 0.036) and volume (p = 0.014).

5.3.2 Above- and Below-Ground Biomass

A similar treatment ranking of the growth characteristics was evident in the mass of the above-ground and coarse root components, and the sum of the above- and below-ground components; the IF treatment accumulated the greatest biomass in these fractions, followed by the I and F treatments, and the control (Table 5.2). The individual treatment effects were not significant, but have been mentioned to highlight similar trends that were observed in the measured growth responses.

Table 5.2 Soil, forest floor, and above- and below-ground biomass pools (kg ha^{-1}) of a four-year-old *E. grandis* stand subjected to various treatments (C = control, I = irrigated, F = fertilised and IF = irrigated and fertilised). Values presented are means and (standard error of the means).

Component		**C**	**I**	**F**	**IF**
Foliage		4706 (129)	5704 (177)	5636 (76)	5902 (413)
Branches	Live	10 478 (226)	11 703 (351)	11 121 (159)	12 198 (662)
	Dead	7400 (265)	7283 (333)	7641 (98)	7557 (162)
Bark		5107 (112)	5785 (168)	5433 (78)	6025 (345)
Stem		39 292 (879)	44 903 (1292)	41 860 (604)	46 737 (2762)
Total above-ground mass		**66 982** (1425)	**75 378** (2132)	**71 691** (1001)	**78 419** (4322)
Coarse roots		5146 (115)	5556 (184)	5428 (74)	5796 (269)
Fine roots	Live	680 (312)	571 (265)	192 (85)	776 (148)
	Dead	499 (152)	469 (335)	343 (113)	403 (176)
Total below-ground components		**6325** (414)	**6596** (698)	**5964** (211)	**6975** (219)
Total above- and below-ground biomass		**73 308** (1311)	**81 974** (2445)	**77 655** (1087)	**85 394** (4527)
Forest floor	Non-woody	2076 (303)	2401 (408)	2057 (263)	2319 (263)
	Woody	4847 (569)	4655 (495)	4611 (822)	5242 (1129)
Soil[1]	0.0 – 0.3 m		3835×10^3	(218×10^3)	
	0.3 – 0.6 m		3862×10^3	(476×10^3)	
Total of all components		$\mathbf{7777 \times 10^3}$ (1360)	$\mathbf{7786 \times 10^3}$ (2475)	$\mathbf{7781 \times 10^3}$ (1480)	$\mathbf{7790 \times 10^3}$ (5454)

[1] Values in parentheses are standard deviations.

Dead branch mass was most accurately predicted using tree height, and although the regression was significant, these two variables were not that well correlated (R^2 = 0.56). There was no clear treatment effect on the dead branch fraction as was observed with other above-ground components, but fertilisation resulted in a slightly higher dead branch mass (7599 kg ha^{-1}) compared to non-fertilised trees (7342 kg ha^{-1}). Cromer and Williams (1982) observed a poor correlation between dead branch mass and basal area of fertilised *E. globulus* trees in Australia. This was attributed to the ability of eucalypts to self-prune dead branches, a process that appears random and often depends on wind or mechanical abrasion (Cromer and Williams, 1982).

Across all treatments, stemwood constituted the greatest proportion of above-ground mass (59%), followed by branches (26%), bark (8%) and foliage (7%). In irrigated (I and IF) treatments, significantly (p = 0.030) more above-ground biomass was allocated to the stem, compared to non-irrigated (C and F) trees, with stem: above-ground mass ratios of 57.6 and 56.2%, respectively. Fertiliser significantly increased foliage mass (fertilised trees produced 5769 kg foliage ha^{-1} compared to 5205 kg ha^{-1} in non-fertilised trees; p = 0.045). Irrigation produced trees with significantly higher foliage (p = 0.029), live branch (p = 0.020), bark (p = 0.014), stem (p = 0.012), total above-ground (p = 0.018) and total above- and below-ground biomass (p = 0.016) compared to trees which did not receive additional water. These respective values were 5803, 11 950, 5905, 45 820, 76 898 and 83 684 kg ha^{-1} in irrigated, versus non-irrigated trees: 5171, 10 799, 5270, 40 576, 69 337 and 75 481 kg ha^{-1}. Irrigated trees had a higher coarse root mass (5676 kg ha^{-1}) compared to non-irrigated trees (5287 kg ha^{-1}), an effect that was weakly significant (p = 0.059). Root:shoot ratios were calculated as coarse root mass: above-ground mass, and a weakly significant (p = 0.074) fertiliser effect was evident, which resulted in a lower root:shoot ratio (7.8%) than in non-fertilised trees (8.0%). The lowest amount of fine roots (live and dead) was observed in the F treatment, amounting to a total fine root mass of only 535 kg ha^{-1}, compared to the I treatment (1041 kg ha^{-1}), and the control and IF treatment (1179 kg ha^{-1}). The IF treatment had the greatest live fine root mass (776 kg ha^{-1}), and the highest dead fine root mass occurred in the control (499 kg ha^{-1}) (Table 5.2).

5.3.3 Forest Floor

The forest floor accumulation under *E. grandis* did not vary greatly with nutrient or water addition (Table 5.2) although the imposed treatments resulted in a greater mass

(7309 and 7115 kg ha^{-1} with irrigation, and fertilisation, respectively, compared to 6796 and 6990 kg ha^{-1} where these treatments were not applied). The lowest woody and non-woody forest floor mass was measured in the F treatment, whereas the highest non-woody forest floor mass accumulated under the I trees, and the greatest woody fraction occurred in the IF treatment.

5.3.4 Soil

Soil masses of 3835 x 10^3 and 3862 x 10^3 kg ha^{-1} were reported for the 0.0 – 0.3 m and 0.3 – 0.6 m depths, respectively, across all treatments (Table 5.2).

The total mass of all the components combined (i.e. the sum of the above- and below-ground biomass fractions, the forest floor and soil pools) increased in the following order: C, F, I and IF (Table 5.2). Irrigation produced significantly (p = 0.025) higher total biomass pools (7788 x 10^3 kg ha^{-1}) compared to non-irrigated treatments (7779 x 10^3 kg ha^{-1}).

5.3.5 Nitrogen Pools

The N content of the various components of the *E. grandis* stand is shown in Table 5.3.

Table 5.3 Nitrogen content (kg ha^{-1}) of the soil, forest floor, and above- and below-ground biomass pools in a four-year-old *E. grandis* stand subjected to different treatments (C = control, I = irrigated, F = fertilised and IF = irrigated and fertilised). Values presented are means and (standard error of the means).

Component		C	I	F	IF
Foliage		98.9 (2.7)	110.1 (3.4)	109.3 (1.5)	109.7 (7.7)
Branch	Live	28.4 (0.6)	39.2 (1.2)	23.5 (0.3)	35.1 (1.9)
	Dead	16.4 (0.6)	18.6 (0.9)	20.3 (0.3)	17.3 (0.4)
Bark		20.3 (0.5)	21.7 (0.6)	20.4 (0.3)	21.4 (1.2)
Stem		33.7 (0.8)	81.5 (2.3)	63.6 (0.9)	63.1 (3.7)
Total above-ground N content		**197.7** (4.4)	**271.1** (7.4)	**237.1** (3.3)	**246.5** (14.8)
Coarse roots		20.5 (0.5)	11.1 (0.4)	16.4 (0.2)	20.6 (1.0)

Table 5.3 (continued)

Component		C	I	F	IF
Fine roots	Live	3.2 (1.0)	4.0 (2.0)	1.0 (0.3)	4.5 (0.7)
	Dead	2.9 (0.6)	2.6 (1.8)	2.8 (1.2)	3.6 (1.5)
Total below-ground N content		**26.6** (1.5)	**17.7** (4.0)	**20.1** (1.4)	**28.7** (1.3)
Total above- and below-ground N content		**224.3** (3.9)	**288.8** (8.3)	**257.2** (3.5)	**275.2** (15.7)
Forest floor	Non-woody	25.2 (5.1)	23.6 (3.0)	27.6 (2.6)	28.4 (3.5)
	Woody	22.0 (4.0)	13.5 (1.8)	17.9 (6.7)	20.7 (3.1)
Total soil N[1]	0.0 – 0.3 m	10 561 (998)			
	0.3 – 0.6 m	5676 (552)			
Total of all components		**16 509** (6)	**16 563** (11)	**16 540** (11)	**16 562** (19)

[1] Values in parentheses are standard deviations.

Irrigation produced significantly higher N contents in the live branches ($p < 0.001$), total branch fraction ($p < 0.001$) and the total sum of all the components ($p = 0.016$) of the *E. grandis* stand. In the absence of irrigation, these respective N contents were 26, 44 and 16 525 kg N ha^{-1}, compared to 37, 55 and 16 563 kg N ha^{-1} where irrigation was applied. A weakly significant ($p = 0.098$) irrigation effect was observed in the live fine root pool, with N contents of 4.3 and 2.1 kg N ha^{-1} in those treatments with, and without irrigation, respectively.

5.3.6 Phosphorus Pools

The P contents of the soil, forest floor and above- and below-ground pools of the *E. grandis* stand are presented in Table 5.4. Irrigation produced significantly higher P contents in the dead branch ($p < 0.001$), bark ($p < 0.001$), stem ($p < 0.001$), above-ground ($p = 0.025$), total fine root ($p = 0.010$), total below-ground ($p < 0.001$), total above- and below-ground pools ($p = 0.009$), and the total sum of all the components ($p = 0.020$) of the *E. grandis* stand, in comparison to non-irrigated plots.

Table 5.4 Phosphorus content (kg ha^{-1}) of the soil, forest floor, and above- and below-ground biomass pools in a four-year-old *E. grandis* stand subjected to different treatments (C = control, I = irrigated, F = fertilised and IF = irrigated and fertilised). Values presented are means and (standard error of the means).

Component		C	I	F	IF
Foliage		6.3 (0.2)	8.2 (0.3)	9.0 (0.1)	7.2 (0.5)
Branch	Live	6.5 (0.1)	5.8 (0.2)	3.7 (0.1)	4.1 (0.2)
	Dead	1.2 (0.04)	1.5 (0.07)	1.0 (0.01)	1.2 (0.03)
Bark		2.8 (0.06)	3.5 (0.10)	2.3 (0.03)	3.3 (0.19)
Stem		6.4 (0.1)	8.2 (0.2)	6.6 (0.1)	7.6 (0.4)
Total above-ground P content		**23.3** (0.5)	**27.1** (0.7)	**22.6** (0.3)	**23.4** (1.4)
Coarse roots		1.3 (0.03)	1.5 (0.05)	1.2 (0.02)	1.8 (0.09)
Fine roots	Live	0.7 (0.10)	0.8 (0.10)	0.6 (0.00)	0.7 (0.03)
	Dead	0.5 (0.03)	0.8 (0.00)	0.6 (0.00)	0.6 (0.07)
Total below-ground P content		**2.5** (0.09)	**3.2** (0.10)	**2.4** (0.02)	**3.2** (0.14)
Total above- and below-ground P content		**25.8** (0.5)	**30.3** (0.7)	**25.0** (0.3)	**26.5** (1.5)
Forest floor	Non-woody	1.5 (0.4)	1.8 (0.3)	1.9 (0.2)	2.0 (0.3)
	Woody	1.1 (0.2)	1.0 (0.1)	1.1 (0.2)	1.1 (0.2)
Total soil P[1]	0.0 – 0.3 m	12 867 (679)			
	0.3 – 0.6 m	6961 (1351)			
Total of all components		**19 857** (1)	**19 862** (1)	**19 857** (1)	**19 859** (2)

[1] Values in parentheses are standard deviations.

5.4 DISCUSSION

The foliage, branch, bark and stem biomass pools were consistent with values cited for three- to nine-year-old *E. grandis* from South Africa (du Toit, 2003; Herbert, 2003), Australia (Bradstock, 1981; Birk and Turner, 1992) and Brazil (Ferreira *et al.,* 1984), which ranged from 3200 – 5600 kg ha^{-1} (foliage), 3200 – 12 940 kg ha^{-1} (total branch), 2400 – 30 170 kg ha^{-1} (bark) and 10 400 – 125 870 kg ha^{-1} (stem). This wide range in biomass pools is not surprising given the broad age bracket and the range of conditions under which these trials were established. As observed in this *E. grandis* stand, irrigated *E. globulus* trees in Portugal allocated a significantly higher proportion of total above-ground biomass to stemwood relative to non-irrigated trees (Pereira *et al.,* 1989; Madeira and Pereira, 1990/91). The treatment response measured in the above- and below-ground biomass in the *E. grandis* stand decreased in the order IF > I > F > C. This trend was consistent with a combination irrigation and fertilisation experiment on *E. globulus* in Portugal (Fabião *et al.*, 1995), indicating that water availability was more limiting to growth than nutrients on both sites.

A rapid decrease in coarse root mass with increasing depth was observed (from approximately 5.0 kg (0.0 – 0.2 m), to 1.0 kg (0.2 – 0.4 m), to 0.5 kg tree^{-1} (0.4 – 0.6 m)). We have no knowledge of the rooting density below 0.6 m, or in the inter-row space, but many other researchers (Chilvers, 1972; Fabião *et al.,* 1990/91; Misra *et al.,* 1998a) have also reported a sharp decline in root density with increasing depth and distance from the tree. In six-year-old irrigated *E. grandis* trees in Australia, approximately 80% of all roots were confined to the 0.0 – 0.3 m soil horizon (Baldwin and Stewart, 1987). We have assumed that about 70 – 80% of the root mass was recovered with the sampling technique used. Ideally, roots should be monitored over time to adequately assess any changes in biomass and nutrient uptake, due to seasonal influence on root growth and turnover through the effects of temperature, moisture and nutrient availability, as observed in a previous study conducted at this site (Nkosana, 2002). The results presented here form a single "snapshot" at the height of the growing season, in an attempt to capture the maximum differences, and hence, illustrate the effects of the treatments. The root masses cannot strictly be compared to those reported in other studies due to the time of year samples were collected and differences in excavation techniques and the depths from which roots were extracted. However, the below-ground mass of these four-year-old trees (6465 kg ha^{-1}) was of the same order of magnitude reported for similar aged *E. grandis* in Brazil, where the root system determined by excavation was approximately 9100 kg ha^{-1} on a poor site compared to 5500 kg ha^{-1} on a good site (Ferreira *et al.,* 1984). Irrigated (I and IF) trees had a higher total root mass than the control and fertilised trees, and the amount of live fine root biomass was much greater in the IF than in the other treatments and the control. Similar responses were reported by Fabião *et al.* (1995) for *E. globulus* in Portugal. O'Connell and Sankaran (1997) tabulated fine-root masses (< 2.0 mm) for a range of species in tropical plantations, with values ranging from 260 – 2100 kg ha^{-1}, compared to 535 – 1179 kg ha^{-1} in this trial.

The forest floor mass accumulated under the trees was 7052 kg ha^{-1}, which is consistent with the reported range (3710 – 6700 kg ha^{-1}) for similar-aged *E. grandis* in Australia (Bradstock, 1981), *E. regnans* in New Zealand (Frederick *et al.,* 1985), and *E. tereticornis* in India (Bargali *et al.,* 1992a). Forest floor accumulation tabulated by O'Connell and Sankaran (1997) over a wide range of *Eucalyptus* species, stand age and location, generally ranged from 800 to 21 600 kg ha^{-1}.

The dry matter distribution between roots and shoots of forest species is determined by the genetic constitution of the trees (Ericsson, 1994a), site quality (Santantonio, 1989), tree age and season (Ericsson *et al.,* 1996), mineral nutrition (Linder and Rook, 1984; Ågren and Ingestad, 1987; Ericsson, 1994a), water availability (Axelsson and Axelsson, 1986; Fabião *et al.,* 1995) and silviculture (Misra *et al.,* 1998a). Assimilates are allocated to shoots under conditions that limit photosynthesis, or to roots if nutrient or water uptake are limited (Cannell, 1985; Ericsson *et al.,* 1996). However, the response to nutrient deficiencies is not uniform, as plants limited by N, P or sulphur allocate more resources below-ground compared to those deficient in K, Mg, Fe or Mn, which exhibit poor root growth (Marschner, 1986; Ericsson *et al.,* 1992). Improvements in silviculture may affect biomass production by increasing the growth of above- and below-ground parts (either with or without a change in the ratio of these components), or by favouring production of one component at the expense of the other, which would not result in an apparent increase in total biomass (Misra *et al.,* 1998a). Binkley (1986) suggested that under high nutrient availability, less allocation to roots may be required, resulting in more carbohydrates for stem growth. There is evidence that reduced allocation to fine roots with improved nutrition is one of the most important processes by which above-ground dry matter production is increased (Cannell, 1985; Axelsson and Axelsson, 1986; Albaugh *et al*., 1998). In this study, a lower amount of total *E. grandis* biomass was allocated to fine roots in fertilised compared to non-fertilised plots (1.1% and 1.5%, respectively). Fertilisation also reduced the proportion of fine roots to total biomass in *P. sylvestris* and *P. abies* stands in Sweden (Axelsson and Axelsson, 1986) and *P. taeda* in the USA (Albaugh *et al.,* 1998).

Axelsson and Axelsson (1986) suggested that water supplied by irrigation during the growing season to Scots pine and Norway spruce in Sweden may reduce the carbon demand of the roots and increase the above-ground net production; a similar effect of improved nutrition. In irrigated *E. globulus* trees in Portugal, a lower fraction of biomass was partitioned to below-ground organs during the early growth stages, and therefore these treatments had a lower root:shoot ratio in comparison to the control (Fabião *et al.,* 1995). The root:shoot ratio of the I treatment was also lower (7.9%) than the control (8.1%) in the *E. grandis* stand in our study.

The fast growth of high-yielding plants makes them nutrient demanding, given the closely-linked processes of growth and nutrient uptake (Ericsson, 1994b; Gonçalves *et al.,* 1997). Total nutrient content depicts variation in tissue age, dry mass, and nutrient concentrations (Madgwick *et al.,* 1981; Frederick *et al.,* 1984). The factors influencing the quantity of nutrients absorbed by trees include the total nutrient demand of the stand, the growth rate of the trees, and the efficiency with which the nutrients are absorbed from the soil (Gonçalves *et al.,* 1997). Soil nutrient availability and subsequent uptake by trees are strongly influenced by the soil moisture status (Gonçalves *et al.,* 1997). The amount and distribution of fine roots and mycorrhizas also play a critical role in the uptake of N and P (Grove *et al.,* 1996; Landsberg and Gower, 1997).

Nitrogen was not considered limiting to growth as the foliar N concentration in all treatments, which ranged from 23.4 – 24.1 mg g^{-1}, closely approximated the recommended value (23.0 mg g^{-1}) for optimal growth. A comparison with the optimum ratios of 7.5 and 33.0 for foliar P:N and K:N, respectively, indicated that these elements were potentially limiting to growth in all treatments. Phosphorus:N ratios were 6.3 (C), 6.4 (I), 6.6 (F) and 6.6 (IF), and K:N values in the C, I, F and IF treatments were 27.2, 28.1, 30.1 and 26.6, respectively. The foliar P to N in the F and IF treatments, and K to N in the F treatment most closely approached the target values. The lowest K:N ratio was observed in the IF treatment, and this was attributed to a dilution effect caused by an increasing leaf biomass (Jarrell and Beverly, 1981). The foliar concentrations of Ca, Mg, Mn, Fe, Zn, Cu and B relative to N exceeded the target values and it was concluded that these elements were not limiting to growth (data not shown).

The N content of the above-ground biomass pools lay within the range reported for foliage (27.0 – 110.0 kg ha^{-1}), branches (6.0 – 63.0 kg ha^{-1}), bark (4.6 – 81.5 kg ha^{-1}) and stem (7.4 – 111.0 kg ha^{-1}) for three- to nine-year-old *E. grandis* growing under various conditions in South Africa (du Toit, 2003) and Australia (Birk and Turner, 1992; Cromer *et al.,* 1993a). For the same reasons given for the biomass of the roots, the N content of this pool cannot strictly be compared to other studies, but the average coarse root fraction (17.2 kg N ha^{-1}) was similar to the 12.4 kg N ha^{-1} obtained by Bargali *et al.* (1992b) for four-year-old *E. tereticornis* in India. Vogt *et al.* (1997) tabulate fractions of total N in the living biomass of roots (including coarse roots) from a range of fast-growing plantation species from 4 – 15%; the values in this trial range from 5 – 11%. Nitrogen accumulation in the forest floor of this four-year-old *E. grandis* stand was 44.7 kg ha^{-1} since stand establishment in comparison to 51.0 kg N ha^{-1} for similar aged *E. regnans* in New Zealand (Frederick *et al.,* 1985). The total soil N pool to a depth of 0.6 m was 16 238 kg N ha^{-1}, which was of the same order of magnitude for an *E. grandis* site in the KwaZulu-Natal Midlands, South Africa (18 650 kg N ha^{-1} to a depth of 0.9 m; du Toit, 2003).

The foliage, bark, branch and stem P pools were comparable to the range of values of 2.3 – 8.1 (foliage), 0.8 – 12.1 (branches), 0.4 – 5.6 (bark) and 0.8 – 13.0 kg P ha^{-1} (stem) reported for three- to nine-year-old *E. grandis* growing under various conditions across South Africa (du Toit, 2003), Australia (Birk and Turner, 1992) and Brazil (Ferreira *et al.,* 1984). The coarse root P content was 1.5 kg ha^{-1}, compared to the range of 1.7 – 16.0 kg ha^{-1} for three- to seven-year-old *E. grandis* in South Africa (du Toit, 2003) and Brazil (Ferreira *et al.,* 1984), although these values cannot strictly be compared because of the differences in excavation techniques. Vogt *et al.* (1997) tabulate fractions of total P in the living biomass of roots from a range of fast-growing plantation species from 7 – 10%, which is identical to the range calculated for these *E. grandis* trees. The P accumulation in the forest floor was 2.9 kg ha^{-1}, which is similar to the 3.9 kg P ha^{-1} measured in a four-year-old *E. regnans* stand in New Zealand (Frederick *et al.,* 1985). The total soil P pool to a depth of 0.6 m was much higher (19 829 kg ha^{-1}) than the value reported by du Toit and Scholes (2002) (4710 kg ha^{-1} to a depth of 1.0 m) for an *E. grandis* stand in KwaZulu-Natal, South Africa. The soil available P pool (79.1 kg ha^{-1}) in the top 0.3 m was an order of magnitude higher than the 7.0 kg P ha^{-1} value reported by du Toit (2003) for the top 0.4 m. These high soil P values are attributed to the site being established on land previously used for agriculture and the possibility that the soil was enriched with P. The total N and P accumulated in 34-month-old *E. nitens* trees in Australia was 290 and 31 kg ha^{-1}, respectively (Misra *et al.,* 1998b), compared to the range of 224 – 289 kg N ha^{-1} and 25 – 30 kg P ha^{-1} in these *E. grandis* trees.

Nutrient concentrations in foliage are higher than any other plant component except the fine roots (Ericsson, 1994a). This was observed in these *E. grandis* trees, where the N concentration (data not shown) in the above- and below-ground components, averaged across the four treatments, was highest in the foliage, followed by the dead and live fine roots, bark, coarse roots, live and dead branches and the stem. The corresponding order for P was foliage, live and dead fine roots, bark, live branches, coarse roots, stem, and dead branches. Leaves are metabolically active and therefore contribute a greater proportion to the nutrient pool compared to other components (Bargali *et al.,* 1992b; Fölster and Khanna, 1997). The foliage accounted for only 7% of the total biomass but contained more than 40% of the total tree N and almost 30% of the total tree P. Nutrient concentrations are lowest in the stemwood of eucalypts, but relative to other biomass fractions, the nutrient mass of the stemwood is large and this fraction forms a major sink for all nutrients (Judd *et al.,* 1996a). Despite the low concentrations in the stemwood of *E. grandis*, this component accounted for 23% of the total tree N, and 27% of the P across all treatments. The highest N and P contents in the stem were measured in the I treatment, driven by the high biomass accumulation in these trees compared to the control and F treatment, but determined mainly by the concentration of these elements in this biomass component. The N concentration in the stem of the irrigated-only trees was 0.18%, compared to 0.09, 0.15, and 0.13% in the control, F and IF treatments, respectively. The highest stemwood P concentration was also measured in the I trees (0.018%), in comparison to the control (0.016%), F (0.016%) and IF (0.016%) treatments. Responses to fertilisation decline with increasing water deficit (Pereira *et al.,* 1996), which could explain the greater biomass and N and P accumulation in the I compared to the F treatment. An increased nutrient uptake occurred in the irrigated-only plots of *E. grandis* in India (Hunter, 2001), and irrigation resulted in a temporary improvement in nutrition of *P. sylvestris* in Sweden (Axelsson and Axelsson, 1986). In addition, the P concentration in the stemwood of irrigated-only *E. globulus* trees in Portugal was much higher than in the control and almost as high as in the fertilised trees (Pereira *et al.*, 1994). Pereira *et al.* (1989) suggested that increased soil moisture in the irrigated *E. globulus* treatments in Portugal increased the amount of available nutrients and the volume of soil explored by the roots.

Nitrogen and P uptake can be enhanced by ectomycorrhizas, by i) an increase in the surface area of the roots (Vogt *et al.,* 1997), and ii) solubilisation of P from relatively insoluble sources in the soil by phosphatase production, and the utilisation of N from organic sources (Harley and Smith, 1983; Bolan, 1991). The soil volume explored is increased by fungal hyphae, which is particularly important for less-mobile nutrients such as phosphate (Miller and Donahue, 1990). Fertilisation with N and P may have a direct effect on the mycorrhizal associations by eliminating the symbiont from the root (Vogt *et al.,* 1997). It is possible that mycorrhizal formation on the F and IF trees was reduced by fertilisation, and this may account for the lower N and P concentrations measured in the

IF versus I treatment. Unfortunately, however, mycorrhizal colonisation was not investigated in this study.

5.5 CONCLUSION

The growth data and biomass pools measured in the above- and below-ground components of this four-year-old *E. grandis* stand indicated that water was potentially more limiting to growth than nutrient availability. Irrigation increased growth across all measured responses and resulted in the highest accumulation of above- and below-ground biomass. Almost all of these responses were significant. Fertilisation produced significantly higher foliage biomass, but the effect was not as great as that caused by irrigation. The lower root:shoot ratio in fertilised (F and IF) trees indicated that proportionally less mass was allocated to below-ground components compared to non-fertilised (C and I) trees. The irrigated (I and IF) trees allocated a significantly higher proportion of total above-ground biomass to stemwood relative to non-irrigated (C and F) trees.

Higher N and P pools were measured in the irrigated compared to non-irrigated trees. The N and P contents measured in this *E. grandis* stand were of the same order of magnitude, but more N than P was accumulated in the tree component. It is anticipated that if tree response to treatment is maintained until clear-felling, harvesting stems from the irrigated plots will remove the greatest amount of N and P compared to where irrigation was not applied.

These estimates of the biomass and N and P pools contained in this *E. grandis* stand specifically addressed the second objective and associated key questions. After four years, the IF treatment accumulated the greatest biomass, followed by the I and F treatments, and the control. The foliage and above-ground woody biomass data were used as part of a model validation exercise. Model validation is essential to test the performance of a model, and to build user confidence in the accuracy of the model outputs. Improving the predictions of growth and water use in plantations is viewed by the South African forest industry as an important research goal (Dye *et al*., 2004). This can be achieved by means of process-based productivity models, which are commonly used for growth analysis and prediction. One such model, 3-PG, has shown considerable potential as a tool for predicting forest productivity. The 3-PG model was validated using data collected from this irrigation and fertilisation trial. Results from this validation exercise are presented in Chapter 6.

CHAPTER 6

APPLICATION OF THE 3-PG MODEL TO A *EUCALYPTUS GRANDIS* STAND SUBJECTED TO VARYING LEVELS OF WATER AND NUTRITIONAL CONSTRAINTS[3]

6.1 INTRODUCTION

In South Africa, estimates of growth and yield are determined using statistically-derived, empirically-based stand-level models. Such models predict plantation growth and yield as a function of stand age, site index and stand density (Kassier and Kotze, 2000). Empirical growth models provide accurate predictions of yield when applied to the conditions for which they were originally developed (Kassier and Kotze, 2000; Landsberg, 2003a). However, these models cannot simulate the results of changing environmental or management conditions (Battaglia and Sands, 1997, 1998), or predict the effects of silvicultural operations such as fertilisation and irrigation (Bergh *et al.*, 1999).

In contrast to empirical models, process-based models are more flexible and can be used with greater confidence to extrapolate experimental results and investigate consequences of conditions outside the range of those experienced in the original experimentation, once adequate testing has been conducted (Landsberg, 1986b). Process-based, or mechanistic models simulate stand growth in terms of the underlying physiological processes or mechanisms that govern growth, and the way stands are affected by the physical conditions to which trees are subject to, and with which they interact (Landsberg and Gower, 1997; Landsberg *et al.*, 2001). Process-based models were originally developed for research purposes, but other applications include (1) prediction of growth and yield from existing plantations, (2) site-species matching, (3) exploration of the effects of different silvicultural practices on the utilisation of site resources, (4) assessment of risks associated with plantation locations or management decisions, (5) evaluation of the effects of events such as fertilisation and thinning, (6) improved understanding of production constraints and growth potential of a site, and

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(7) questions for which ‘real time’ experiments are not feasible, such as long-term impacts of practices on sustainability (McMurtrie *et al.*, 1990; Battaglia and Sands, 1998; Landsberg, 2003a). However, few process-based productivity models are adopted for forest management systems as they are complex, poorly validated, and the details of many fundamental processes, such as carbon allocation, remain uncertain (Battaglia and Sands, 1998). In addition, these models require large amounts of input data, and parameter values are not readily available or economically obtainable (Landsberg *et al.*, 2001; Landsberg, 2003a). More generalised and simplified process models, such as 3-PG, have been developed specifically to bridge the gap between conventional, empirical, mensuration-based growth and yield models, and process-based carbon balance models (Johnsen *et al.*, 2001; Sands and Landsberg, 2002; Landsberg, 2003a,b).

The 3-PG (Physiological Principles Predicting Growth; Landsberg and Waring, 1997) model can realistically simulate growth and water use over a wide range of rotation age and growth conditions (Dye *et al.*, 2004), and has been identified as an ideal tool to determine site constraints on growth and potential productivity over a range of sites (Esprey and Sands, 2004). This model has yielded credible predictions for a wide range of species across several countries, e.g. Australia and New Zealand (Landsberg and Waring, 1997; Coops *et al.*, 1998; Sands and Landsberg, 2002), Brazil (Almeida *et al.*, 2004a; Stape *et al.*, 2004b), Chile (Rodríguez *et al.*, 2002), USA (Coops and Waring, 2001; Landsberg *et al.*, 2001), South Africa (Gush, 1999; Dye, 2001; Esprey and Smith, 2002; Dye *et al.*, 2004), and Sweden (Landsberg *et al.*, 2003). In addition to 3-PG’s widespread application, this model was selected as the most appropriate for use as it was developed with the end user in mind, is robust with a simple and transparent structure, is extensively documented (see Sands, 2004), data inputs are readily obtained, outputs are of interest to the forest manager, and the model and source-code are freely available.

Model validation is important to test the performance of the model in predicting growth and productivity. Many tests against good measurements of stem growth rates, *L*, stand biomass, average stem diameter and sap flow data should be conducted as a means of validating model outputs (Landsberg and Waring, 1997; Sands and Landsberg, 2002; Landsberg *et al.*, 2003). Various aspects of the 3-PG model have been tested, e.g. stem diameter and volume growth (Landsberg *et al.*, 2001; Rodríguez *et al.*, 2002; Almeida *et al.*, 2004a), *L* and above- and below-ground biomass (Landsberg *et al.*, 2003), stem number and available soil water (Coops and Waring, 2001; Dye, 2001), and sap flow rates (Dye *et al.*, 2004).

The principal objective of this study was to validate the 3-PG model using the parameter set developed by Esprey and Sands (2004), by applying the model to biomass data collected from this irrigation and fertilisation trial. The 3-PG model was validated by testing both the primary outputs of the model, i.e. *L* and above-ground biomass partitioning, and those outputs of relevance to forestry management, such as stand volume. This study builds on the earlier work conducted by Gush (1999), Dye (2001), Esprey and Smith (2002) and Dye *et al.* (2004), who demonstrated the potential use of 3-PG as a tool for modelling South African forest productivity. The novel contribution from this study is the application of 3-PG to trees subjected to irrigation and fertilisation treatments, which could aid in scenario analysis and planning, and the development of fertiliser recommendations.

6.2 MATERIALS AND METHODS

6.2.1 Site Description and Experimental Design

A description of the site is given in Section 3.1, and the experimental design and imposed treatments are presented in Section 3.3.

6.2.2 Measurements and Sampling

Stem DBH and tree height data were collected on a routine basis, approximately four times per year, and used to calculate stem volume to 5 cm underbark diameter, using the Schumacher-Hall equation as described in Coetzee (1992). Estimates of above-ground biomass and partitioning were obtained from destructive harvests carried out when the trees were aged approximately two, three and four years. Sample trees (n = 4, 4, and 6 trees per treatment for each of the three destructive harvests, respectively) were selected to represent the range in DBH at the time of harvesting. The representative trees were felled at ground level and separated into stem, foliage, and total branches (live and dead). Each stem was measured for total length (height) and sample disc sections were cut at 1 m intervals to determine the ratios of stemwood and stembark. The fresh mass of all material was measured in the field by weighing both the total mass and a representative sub-sample, which was returned to the laboratory for dry mass determination at 70 °C. The fresh:dry mass ratios were used to estimate total dry mass of the various components. The leaf areas of foliar sub-samples were determined by scanning using a LI-3100 Area Meter (LI-COR Inc., Lincoln, Nebraska, USA). These leaf area measurements were used for the calculation of specific leaf area (*SLA*; leaf area per unit dry leaf mass) and hence *L* (leaf area per unit ground surface area). Allometric relationships of the form $y = ax^b$, where y = mass and *x* = DBH, were developed to derive biomass estimates of above-ground components for each treatment.

6.2.3 The 3-PG Model

3-PG is a stand-level model of forest growth (i.e. it is not site- or species-specific, but needs to be parameterised for individual species) (Sands and Landsberg, 2002; Landsberg, 2003b). Since the initial publication of 3-PG (Landsberg and Waring, 1997), several structural modifications have been made to the model, and the manner in which various relationships between parameters are depicted has been changed to make the parameters more intuitively meaningful; these are summarised in Sands and Landsberg (2002). The most recent changes to the model are presented by Sands (2004).

The structure of the 3-PG model is comprehensively described in the literature (Landsberg and Waring, 1997; Sands and Landsberg, 2002; Landsberg *et al.*, 2003) and only a brief summary will be provided here. The 3-PG model is based on the fraction of photosynthetically active radiation absorbed by the forest canopy, and consists essentially of two sets of calculations; biomass production, and the subsequent allocation of biomass between the component parts of the tree. 3-PG also contains sub-models relating to the calculation of soil water balance, evapotranspiration and tree mortality.

In the 3-PG model, the conversion of absorbed photosynthetically active radiation to GPP is based on a theoretical maximum canopy quantum efficiency constrained by various environmental modifiers (*D*, available soil water, temperature, frost, site nutrition and stand age; Sands and Landsberg, 2002). These modifiers are applied multiplicatively, with the most limiting of the atmospheric *D* and soil water factors being used, i.e. if soil water is more limiting than *D*, growth is assumed to be constrained by soil water during that period (Landsberg *et al.*, 2001; Sands and Landsberg, 2002). Net primary production in 3-PG is calculated as a constant fraction of GPP (see Waring *et al.*, 1998), which is then allocated to roots, stems and foliage (Landsberg *et al.*, 2001).

The proportion of NPP allocated to roots increases if nutritional status and/or available soil water are low, and allocation to stems and foliage is reduced such that the allometric balance of the trees is conserved (Landsberg and Waring, 1997; Landsberg *et al.*, 2001).

Mandatory inputs required by 3-PG are monthly weather data (average values of daily solar radiation and temperature, atmospheric *D*, total rainfall and the number of frost days per month), site-specific factors, initial stand conditions and species-specific parameter values. The model can be run for any number of years, using actual monthly weather data or long-term monthly averages. Using historical long-term averages is the normal procedure unless there is particular interest in specific events, such as droughts (Landsberg *et al.*, 2001). Site-specific factors in 3-PG which describe the physical properties of the site include latitude, a site fertility rating (*FR*), maximum available soil water and a general descriptor of soil texture. The *FR* accounts for the nutrition of the site, and varies between 'poor' (*FR* = 0) and 'optimal' (*FR* = 1) nutrient status. The effects of nutrition enter the 3-PG model through influences on canopy quantum efficiency and biomass allocation and therefore fertility is a potentially important input variable. Despite many years of worldwide research efforts on this subject, our ability to predict soil nutrient status in terms usable in quantitative models of plant growth is extremely limited (Landsberg *et al.*, 2001). Ingestad (1982, 1991) addressed the dynamic nature of the underlying relationships between nutrition and growth, which vary with climatic conditions (Negi and Sharma, 1996), soil processes which regulate nutrient quantities in soil solution, the amount and distribution of fine roots and mycorrhizas (Landsberg and Gower, 1997), the efficiency with which nutrients are absorbed from the soil, the total nutrient demand of the stand, and the growth rate of the trees (Gonçalves *et al.*, 1997). Plant analyses can be used as an indirect measure of the fertility status of soils and the efficiency of fertilisation events (Melsted *et al.*, 1969). In 3-PG, *FR* values are usually allocated on the basis of local knowledge about soil fertility (Landsberg, 2003a).

The stand initialisation data in 3-PG include the year and month of planting, the initial stand age and the age at the end of the rotation, the foliage, root and stem biomass, soil water-holding capacity in the root zone, and initial stem number appropriate to the stand at the starting age. The species-specific parameter values pertain to allometric relationships, canopy structure and processes, wood and stand properties, stem mortality, litterfall and root turnover, and the various environmental modifiers.

The 3-PG model can be initialised for any stand age, although the normal procedure is to start simulations from the second year of growth (Landsberg *et al.*, 2003). In 3-PG, the state of the stand is updated at each monthly time step. The primary output variables from the model include monthly or annual values of NPP, foliage, root and stem biomass, stem number, available soil water and stand transpiration, and of value to forest managers – DBH, *L*, stand volume and mean annual increment (Sands and Landsberg, 2002). Given the appropriate geometrical relationships, 3-PG can also provide estimates of stand height (Landsberg *et al.*, 2003), although this component of the model still needs to be tested.

6.2.4 Model Inputs

6.2.4.1 Weather data

Long-term monthly mean solar radiation data were obtained from the digital database developed by Schulze (1997). Actual monthly temperature data were collected from an automatic weather station situated at a nearby research site in the Seven Oaks district (see Section 3.4.1). A Campbell Model 207 temperature and relative humidity sensor (Campbell Scientific, Inc., 815W. 1800 N., Logan, UT 84321-1784, USA) was used to record temperature, and a Campbell 21X data logger was programmed to log the data at 20 minute intervals, which were averaged over a 12-hour period each day. The 3-PG model calculates mean air temperature and *D* from mean minimum and maximum air temperatures. Real-time monthly rainfall data were extracted from a raster database (Lynch, 2003; see Section 3.4.1). Irrigation amounts were added to the rainfall in the I and IF treatments.

6.2.4.2 Initialisation data

The 3-PG model predicts growth from the time of stand establishment, but the accuracy for young trees prior to canopy closure may be significantly in error (Landsberg and Waring, 1997; Landsberg, 2003a). Therefore, 3-PG was initialised at age two, and model runs were conducted for a two-year period. The mean maximum available soil water content was determined on a per treatment basis as 151 mm (C), 128 mm (I), 112 mm (F) and 84 mm (IF), calculated as the product of soil depth and texture-derived available water capacity (Smith *et al.*, 2004; Table 6.1).

Table 6.1 Total soil depth and available soil water content of the control (C), irrigated (I), fertilised (F) and irrigated and fertilised (IF) treatments.

Soil component	C	I	F	IF
Total soil depth (m)	0.95	0.78	0.68	0.50
Available water capacity (mm m^{-1})	160	160	160	160
Total available water (mm)	151	128	112	84

Fertility rating values of 0.6, 0.7, 0.8 and 0.9 were specified for the C, I, F and IF treatments, respectively. In this study, soil chemical characteristics at the start of the experiment were used in conjunction with foliar nutrient analyses to assign *FR* values. Prior to treatment implementation, the surface soil contained high concentrations of available P, organic carbon and total N (Table 3.1). The relative fertility of the site was the justification for setting the *FR* value of the C treatment at 0.6. Over the simulation period from two to four years of age, the foliar P:N and K:N ratios of the F and IF treatments closely approximated the target values only in February 2002 (aged 3.1 years). These P:N ratios were 7.2 (F) and 7.6 (IF), with associated K:N values of 32.7 and 33.4. A comparison across all treatments over the remainder of the simulation indicated that P and K were potentially limiting to growth when compared with the optimum ratios of 7.5 and 33.0 for P:N and K:N, respectively. The foliar N concentration in all treatments closely approximated or was higher than the recommended value for optimal growth (23.0 mg g^{-1}). The concentrations of Ca, Mg, Mn, Fe, Zn, Cu and B relative to N exceeded the target values in all treatments and it was concluded that these elements were not limiting (data not shown).

Due to the possible limitation of P and K at the site, the *FR* value of the F treatment was set at 0.8, in contrast to a value of 1.0, which would indicate optimal nutrient status. Soil nutrient availability and uptake by trees are strongly influenced by the soil moisture status (Gonçalves *et al.*, 1997), with reduced uptake under dry soil conditions (Landsberg and McMurtrie, 1985). Many studies have shown increased nutrient accumulation as a result of irrigation (Axelsson and Axelsson, 1986; Madeira and Pereira, 1990/91; Pereira *et al.*, 1994; Hunter, 2001). For this reason, the *FR* of the I and IF treatments was set at a 0.1 unit higher than their respective non-irrigated counter-parts. Fertilisation can be incorporated as a silvicultural event in 3-PG, i.e. temporal changes in *FR* can be specified. Due to our limited understanding of the complex interactions between factors and processes governing nutrient availability and uptake at this site, we used a static *FR* input into the model.

Using observed data, initial foliage and stem biomass values were assigned, with root biomass estimated as approximately 25% of total tree biomass (Shepherd, 1985). These data are presented in Table 6.2.

Table 6.2 Biomass values of *E. grandis* entered as input data into the 3-PG model. C = control, I = irrigated, F = fertilised and IF = irrigated and fertilised; W_F, W_R, and W_S refer to the foliage, root and above-ground woody biomass (stem wood plus bark and branches), respectively. W_R was estimated as approximately 25% of total tree biomass (Shepherd, 1985).

Treatment	W_F (t ha^{-1})	W_R (t ha^{-1})	W_S (t ha^{-1})
C	3.0	4.7	11.1
I	3.4	5.9	14.4
F	3.7	6.1	14.7
IF	4.3	7.9	19.4

Parameter values used in the model simulations are listed in Esprey and Sands (2004). Based on measurements at the site, *SLA* at the initial stand age was reduced from 13 to 11. Parameters used in the calculation of mortality were adjusted to account for the reduction in stem number following the two wind storms. All other parameters remained unchanged. Model runs were made with $3PG_{PJS}$, a user-friendly interface to 3-PG, developed as Visual Basic macros using Excel spreadsheets (Sands, 2004).

6.2.5 Model Performance

3-PG model-performance can be evaluated through assessing the correlation between observed and simulated values (R^2) (Esprey and Smith, 2002; Landsberg *et al.*, 2003; Almeida *et al.*, 2004b; Stape *et al.*, 2004b). In this trial, however, it is unlikely that the small number of data points (n = 4) at any one sampling period would generate a realistic estimate of the correlation between observed and simulated values. Therefore, model predictions of above-ground biomass and *L* were assessed in terms of percent bias, calculated as ((observed – simulated) / simulated)*100, with negative values indicating model over-prediction.

6.3 RESULTS AND DISCUSSION

Using the appropriate weather and initialisation data, site factors, and parameter values as inputs into 3-PG, simulations were carried out for a two-year period and outputs compared against observed above-ground biomass and L values (Figure 6.1).

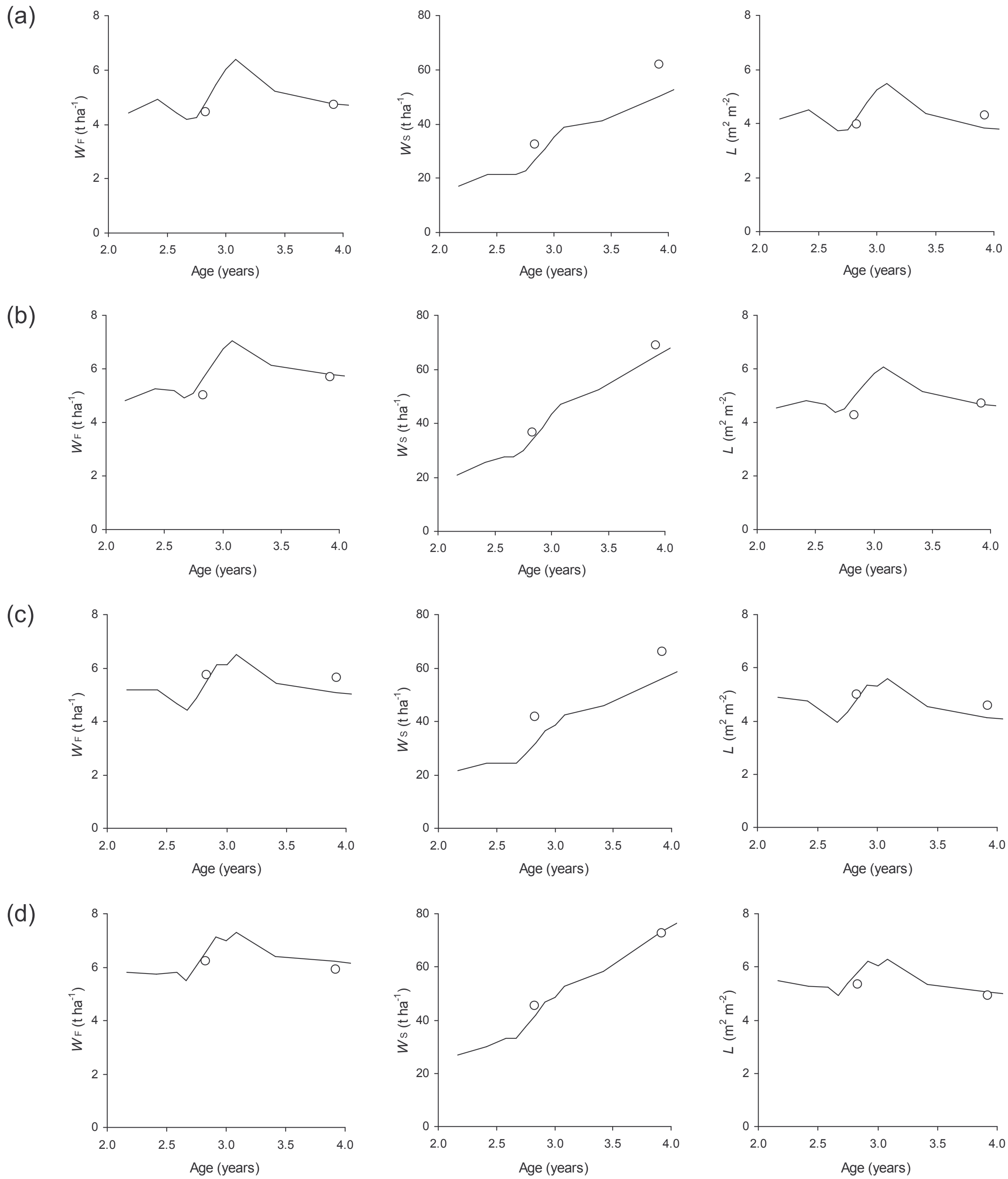

Figure 6.1 Time series of observed (o) and 3-PG model-simulated (—) foliage (W_F) and above-ground woody (W_S) biomass, and leaf area index (L) in (a) control, (b) irrigated, (c) fertilised and (d) irrigated and fertilised *E. grandis* trees.

The 3-PG model accurately predicted foliage (W_F) and above-ground woody (W_s) biomass, and L across all treatments at three and four years. The correspondence between observed and simulated values in the irrigated (I and IF) trees was excellent, particularly at four years. Above-ground woody biomass was consistently under-predicted in the non-irrigated (C and F) treatments. The highest bias values were calculated for W_s in the C and F treatments at both time periods (Table 6.3). In general, the model predictions for these non-irrigated trees were poorer than for irrigated trees. The 3-PG model produced under-predicted values for all variables at both time periods in the F treatment, indicated by the positive bias.

Table 6.3 Percentage bias of model predictions for *E. grandis* trees subjected to various treatments. C = control, I = irrigated, F = fertilised and IF = irrigated and fertilised; W_F and W_S refer to the foliage and above-ground woody (stem wood plus bark and branches) biomass, respectively. L represents the leaf area index.

Output variable	3 years	4 years
	C	
W_F	-8.4	-0.6
W_S	21.8	23.7
L	-7.3	12.3
	I	
W_F	-11.1	-1.6
W_S	8.0	6.1
L	-14.1	0.4
	F	
W_F	4.3	11.1
W_S	31.1	17.5
L	2.9	10.8
	IF	
W_F	-5.8	-5.4
W_S	8.1	-1.2
L	-8.1	-2.9

Leaf area index determines radiation interception, which drives carbon assimilation and stand growth, as well as transpiration rates (Landsberg *et al*., 2001). It is therefore essential to ensure that maximum L produced by a stand, and the time course of this variable are consistent with observations (Landsberg *et al*., 2001). Unfortunately, only two data points for each treatment could be used to compare observed and simulated *L* values, but the close agreement between these increases our confidence that the 3-PG model predictions of growth and biomass data are correct for the right reasons.

Encouraged by the close correspondence between observed and simulated above-ground biomass and *L* values, we used the 3-PG model to predict stand volume (Figure 6.2).

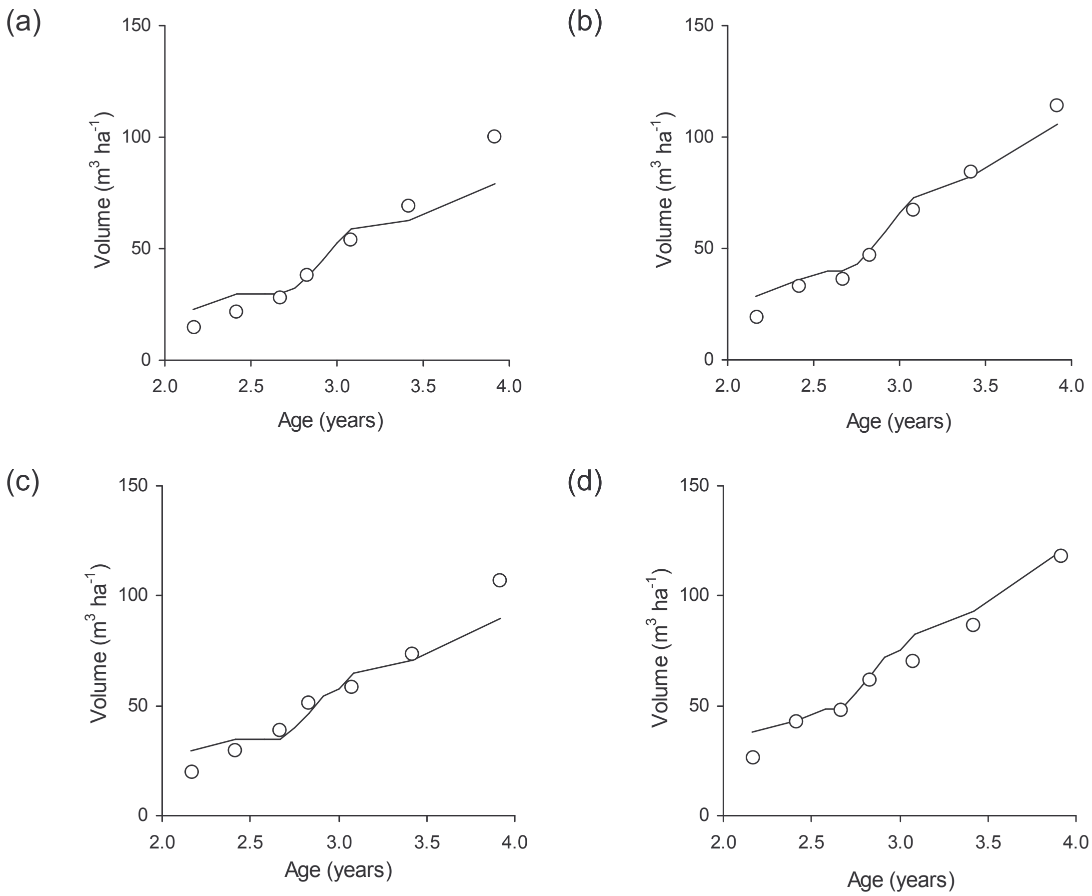

Figure 6.2 Time series of observed (o) and 3-PG model-simulated (—) stand volume in (a) control, (b) irrigated, (c) fertilised and (d) irrigated and fertilised *E. grandis* trees.

In general, there is good agreement between observed and simulated stand volume growth across all treatments. The 3-PG model tends to under-predict stand volume in the non-irrigated treatments at the end of the second simulation year. At this age (four years), simulated stand volume in the C and F trees was 78.9 and 89.6 m^3 ha^{-1}, respectively, compared to observed values of 100.0 and 106.5 m^3 ha^{-1}. In the I treatment, stand volume was slightly under-estimated (105.5 and 113.8 m^3 ha^{-1} for predicted and observed data, respectively), but in the IF treatment, the predicted value (120.8 m^3 ha^{-1}) very closely approximated observed stand volume (118.0 m^3 ha^{-1}).

There are three plausible explanations as to why the 3-PG model under-predicted stand volume in the non-irrigated treatments at age four years. Firstly, it is possible that the C and F trees had access to more water than was estimated. A simulation conducted under the assumption of additional water (approximately 50% of that received by irrigated trees) increased growth to provide a closer approximation to measured values. These predicted stand volumes were 89.8 and 100.6 m^3 ha^{-1} in the C and F treatments, respectively. In a review provided by Knight (1999), it emerged that *Eucalyptus* trees have dimorphic root systems, consisting of wide-spreading lateral roots just below the soil surface, with deep tap roots in young trees and deep vertical sinker roots in mature trees. During dry periods, deep-rooted eucalypts are able to maintain transpiration at rates which enable the trees to function, by accessing water stored in the soil profile (Knight, 1999). The failure of four-year-old *E. grandis* trees to respond to an imposed soil water deficit in Mpumalanga was attributed to their ability to abstract soil water to a depth of at least 8 m (Dye, 1996; Dye *et al*., 1997). Alternatively, trees could access water by means of a vertical water flux: Dye *et al*. (1997) suggested the possibility of an upward movement of water during dry weather, which could supplement soil water availability within the rooting zone. This type of water movement was quantified by Soares and Almeida (2001) to approximate 1 mm day^{-1} at a site in Brazil. This upward flux from the water table into the root zone helped prevent complete stomatal closure and maintained *E. grandis* functioning at approximately 30% of its potential at the end of a long dry season (Soares and Almeida, 2001). If these types of processes occur in this trial, it is unlikely that they will operate to the same extent as the studies mentioned here, due to the lower porosity of the saprolite at this site.

Secondly, the stand volume may have been under-estimated in the non-irrigated treatments if the workings of the soil water module of the model are problematic. Dye *et al*. (2004) checked 3-PG-simulated transpiration rates with observed sap flow data collected from stands of *E. grandis* x *camaldulensis* in the Zululand region. These authors observed a good correspondence between the highest simulated transpiration rates and the measured median daily sap flow rates. However, almost all of the minimum simulated transpiration data points were lower than the observed lowest sap flow rates; Dye *et al*. (2004) attributed this discrepancy to the simple manner in which 3-PG calculates soil water availability. The soil water balance component in 3-PG is a simple, single-layer model obtained as the difference between monthly precipitation and monthly evapotranspiration, calculated using the Penman-Monteith equation (Landsberg and Waring, 1997). The use of a monthly water balance in 3-PG assumes that rainfall is evenly distributed over the month, which obviously does not occur, so that soil depletion and recharge patterns are distorted (Landsberg and Waring, 1997). These authors suggested using a daily water balance model to solve this problem, but also stated that this would increase model complexity and data requirements.

The discrepancy between observed and predicted stand volume in the non-irrigated treatments could also be related to an under-estimation of NPP and/or an under-estimation of NPP allocation to stemwood, which may be attributed to errors in the calculation of soil water or atmospheric *D*, or could result from the assigned *FR* values. In the 3-PG model, adjustments to *FR* influence above-ground biomass production by altering the canopy quantum efficiency and carbohydrate allocation to roots (Landsberg *et al*., 2003). If the nutritional status at four years was higher than the *FR* values of 0.6 and 0.8 specified for the C and F treatments, respectively, allocation to below-ground components would be lower, and as suggested by Binkley (1986), could result in more carbohydrates for stem growth. Esprey *et al*. (2004) showed the moderate sensitivity of stand volume to site fertility. Over- or under-estimation of this variable at particular points in a time series may indicate that the nutritional status was respectively lower, or higher than the static *FR* used as an input into the model. Litterfall N or N mineralisation rates, as well as conventional analyses of soil P content can be used as measures of fertility (Landsberg and Waring, 1997). The development of satisfactory and dependable relationships between *FR* values and conventional measures of soil fertility will probably result from understanding and quantifying foliage response (in terms of mass dynamics and nutrient concentrations) to site fertility and nutrient availability (Landsberg *et al*., 2001). These authors also suggested using dynamic soil organic matter models which may aid in solving the problem of modelling site nutrition and tree nutrient uptake. Stape *et al*. (2004b) recommended the use of paired plots with and without fertiliser in a plantation inventory network over a regional area as an effective tool for estimating *FR* for 3-PG and other process-based models.

Given suitable data, a model intended for management should be recalibrated for local conditions (Sands *et al*., 2000). Some studies have calibrated the 3-PG model for a particular site (Landsberg *et al*., 2001, 2003; Almeida *et al*., 2004a; Stape *et al*., 2004b). At this stage, we do not have the necessary information for calibration of the model to this site. However, we are certain that if adequate data were available, the 3-PG model outputs would have provided an even closer fit to observed values.

Despite the generally good agreement between observed and simulated data, model testing and evaluation on such young (two- to four-year-old) trees may provide limited information about 3-PG's likely performance in older stands. This particular model has been shown to accurately predict growth in mature trees (e.g. Landsberg and Waring, 1997; Landsberg *et al.*, 2001, Rodríguez *et al.*, 2002; Landsberg *et al.*, 2003; Dye *et al.*, 2004).

6.4 CONCLUSIONS

Model testing is imperative to build user confidence in the accuracy of a model. In this study, validation of the 3-PG model was performed using the parameter set developed by Esprey and Sands (2004). Although the observed data from this trial are independent of those used to develop the parameter set, this study does not constitute a complete validation of 3-PG, which would require consideration of the temporal variation of all above- and below-ground biomass pools, and of available soil water (Esprey *et al*., 2004).

Outputs from the 3-PG model have highlighted the need to focus our understanding on how *FR* varies seasonally and with silvicultural regime to provide an objective method for estimating *FR* values. Dynamic allocation patterns between above- and below-ground components in response to site resource availability deserve further investigation. The results have shown 3-PG to be a robust model, producing accurate predictions of tree growth under varying levels of resource availability, using a single parameter set. It is encouraging that the model can predict canopy response (in terms of leaf area) to changes in resource availability, as this is the tree component that ultimately drives growth and water use.

There is much current interest in predicting the maximum amount of water that can be transpired by *Eucalyptus* trees. Modelling provides the best approach to evaluate the effects of climate and soil conditions on the water use of trees, as the various factors influencing transpiration can be assessed. The results presented in Chapter 6 specifically address the third objective and related key question. This information suggests that the water-balance component of the 3-PG model may need to be improved, and that there could be errors in the calculation of soil water or atmospheric *D*. For this reason, the transpiration rates predicted by the 3-PG model were not used to provide an estimate of the water use of the *E. grandis* trees. Instead, sap flow data were measured in one tree from the irrigated-only treatment and used in the development of a model to predict maximum rates of transpiration by *E. grandis* plantations under conditions of non-limiting soil water availability. This model is presented in Chapter 7. It was not possible to validate the stand-level estimates of transpiration by 3-PG with the sap flow data collected from this trial, as it would be inappropriate to scale water use from a tree level up to an entire stand level based on measurements from only a single tree.

CHAPTER 7

MODELLING MAXIMUM CANOPY CONDUCTANCE AND TRANSPIRATION IN *EUCALYPTUS GRANDIS* STANDS NOT SUBJECTED TO SOIL WATER DEFICITS[4]

7.1 INTRODUCTION

There are growing concerns that deep-rooted trees, such as *Eucalyptus*, lower water tables and interfere with regional hydrology (Landsberg, 1997). In South Africa, the water use of *E. grandis* remains a controversial issue due to the perception that eucalypt plantations have the greatest impact on catchment water yields. It is important to obtain good data, and to be able to simulate water use at any given plantation, as only accurate measurements will provide a foundation on which decisions regarding regional ecology and human welfare can be made (Landsberg, 1997). Water use data are also required to evaluate the efficiency with which trees use water. High water use efficiency will be an important feature in increasing plantation yields and returns on investment (Dye, 2000). There is considerable information on the rates of water use by *E. grandis*, from both national (Dye, 1987; Dye and Olbrich, 1993; Olbrich *et al*., 1993; Dye, 1996; Dye *et al*., 1997), and international studies (Myers *et al*., 1996; Kallarackal and Somen, 1997a; Soares and Almeida, 2001). However, due to variations in site quality, there are still insufficient data to predict water use over the full range of growing conditions.

It is particularly important to be able to predict maximum rates of transpiration under conditions of non-limiting soil water availability, as

- Increasingly, fast-growing plantations are being investigated for their potential in disposing of industrial effluent from mines and other industries. It is essential to match applied waste water to the capacity of *Eucalyptus* trees to take up and transpire this water.
- Insufficient information exists on a) how soil fertility and water availability influence water use through canopy development, and b) the acclimation of

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the whole-tree water transport system to the long-term availability of soil water at a given site.

- Some recent evidence from Zululand suggests that these physiological changes may give rise to high rates of transpiration (Dye *et al*., 2004). Soil water deficits are the most common limitation to growth and water use in South African forestry plantations. In order to model these, it is important to know what the potential rate of stomatal conductance (g_s) and transpiration is.

Modelling is the best approach to explore the effects of climate and soil conditions on the water use of *E. grandis,* as the various factors affecting transpiration can be taken into account. Transpiration rates are influenced by atmospheric evaporative demand, soil moisture availability, and canopy conductance (g_c), which in turn is controlled by g_s and leaf area (Waring and Schlesinger, 1985; Beadle, 1997; Landsberg and Gower, 1997). The three predominant environmental controls on g_s at the canopy level are light intensity, *D*, and the water status of the leaves (Landsberg and Gower, 1997). Models have been developed to describe stomatal and/or canopy conductance in response to two of the major environmental influences, light and *D* (Warrit *et al*., 1980; Thorpe *et al*., 1980; Kaufmann, 1982a,b; Dye and Olbrich, 1993; Granier *et al*., 2000). Model estimates of g_c are often used in conjunction with the Penman-Monteith (P-M) equation (Monteith, 1965, 1981) to predict rates of evapotranspiration (Dye, 1987; Green, 1993; David *et al*., 1997; Landsberg and Waring, 1997; Soares and Almeida, 2001). This equation combines the two environmental drivers of evaporation, i.e. net radiation and dryness of the air, with a physical control (boundary layer conductance), and a physiological control (canopy g_s) (Landsberg and Gower, 1997; Waring and Running, 1998).

Predictions of water use by trees must be verified against actual measurements of sap flow, which are commonly conducted using the HPV technique. Experimental trials in the summer rainfall region of South Africa provided a valuable opportunity to measure sap flows under conditions of no soil water deficit, and to investigate the daily variation in g_c and transpiration. A simple model was constructed to predict g_c from the season of year, *D* and solar radiation data collected at one of the sites. The model was tested against g_c calculated from the P-M equation and measured sap flow rates at the second site.

7.2 MATERIALS AND METHODS

7.2.1 Site Descriptions

7.2.1.1 Came

The experiment at Came is described Chapter 3. Sap flow measurements were initiated in August 2001 and only irrigated trees were considered in this particular study. The irrigated treatment received a total of 291 mm water during the August to November measurement period; 243 mm were received as rainfall, and 48 mm were applied as irrigation.

7.2.1.2 Frankfort

The Frankfort trial is located in the vicinity of Sabie, Mpumalanga (Lat. 24^o 49' S, long. 30^o 43' E, alt. 950 m a.s.l.). This trial investigated the relationship between soil water availability and transpiration rates of *E. grandis* plantations, and was initiated in June 1992 in a stand of three-year-old trees planted at a spacing of 3.5 x 3.5 m. The well-drained soil is of granitic origin and is classified as a Hutton (Soil Classification Working Group, 1991). Deep drilling showed the permeable subsoil at this site to extend beyond 30 m (Dye, 1996; Dye *et al*., 1997). The mean annual rainfall is 1459 mm, most of which falls in the summer months. The mean annual temperature is 18.1 ^{o}C. Plastic sheeting was laid out in a 30 x 30 m area centred on four sample trees, with the aim of preventing soil water recharge and inducing a progressive drying of the soil by tree roots. See Dye (1996) and Dye *et al*. (1997) for further details.

7.2.2 Weather Data

The weather data for Came were collected from an automatic weather station situated at a nearby research site in the Seven Oaks district (see section 3.4.1). Sensors at the Seven Oaks weather station recorded temperature and relative humidity (Campbell Model 207 temperature and relative humidity sensor; Campbell Scientific, Inc., 815W. 1800 N., Logan, UT 84321-1784, USA), total solar irradiance (Kipp and Zonen solarimeter, Mercuriusweg 1, 2624 BC Delft, Holland), and rainfall (Rimco tipping bucket rain gauge; Selbys Scientific Ltd., 352 Ferntree Gully Road, Notting Hill, Victoria, Australia 3168). A Campbell 21X data logger was programmed to log data at 20 minute intervals, which were averaged or totalled over a 12 hour period each day. At the Frankfort site, an automatic weather station was mounted on the highest frame of a scaffholding tower erected near the centre of the experimental plot. The height of the tower was periodically increased to a maximum height of 23 m, to maintain it at approximately 1 m above the tallest adjacent tree. Sensors recorded temperature (MCS174 probe; Mike Cotton Systems (Pty.) Ltd., P.O. Box 73, Steenberg 7947, South Africa), relative humidity (Vaisala Humicap sensor; Vanha Nurmijarventie 21, 01670 Vantaa, Finland), solar radiation (pyranometer; LI-200S, LI-COR Inc., Lincoln, Nebraska, USA) and rainfall (Rimco rain gauge). An MCS datalogger was programmed to record hourly means of one minute instantaneous measurements.

7.2.3 Pre-Dawn Xylem Pressure Potential

Pre-dawn xylem pressure potential (XPP) measurements were performed with a Scholander pressure chamber (Ritchie and Hinckley, 1975). At the Came site, sample twigs were cut from the upper third of the canopy of six randomly located trees in the irrigated treatment. At Frankfort, a sample leaf was taken at mid-canopy position from each of five trees within reach of a centrally-located scaffholding tower. Dates on which pre-dawn XPP was measured are listed in Table 7.1.

Table 7.1 Dates on which pre-dawn XPP measurements were conducted at the Came and Frankfort sites.

Came	Frankfort	
2001	**1992**	**1993**
7 Jun	2 Jun	13 Jan
26 Sep	16 Jun	4 Feb
24 Nov	30 Jun	9 Mar
	14 Jul	2 Apr
	28 Jul	18 May
	11 Aug	1 Jun
	25 Aug	15 Jun
	10 Sep	
	22 Sep	
	6 Oct	
	20 Oct	
	3 Nov	
	17 Nov	
	1 Dec	

7.2.4 Sap Flow Measurements

Heat pulse velocity was used to monitor hourly sap flow rates in two adjacent sample trees at Came, and four adjacent sample trees at Frankfort, located at the centre of each site. This technique has been verified on *E. grandis* using the cut-tree method (Olbrich, 1991). Sap flow was measured over a six-month and twelve-month time period at the Came and Frankfort sites, respectively. Four sets of heat pulse probes were implanted in each sample tree at various positions around the trunk. Using a 20 mm-thick drill jig, three vertically aligned holes were drilled radially into the sapwood at each position, using a 1.85 mm drill bit. A line heater was inserted into the central hole, while a teflon tube containing a single thermistor sensor was implanted in each of the other two holes, 10 mm above and 5 mm below the heating probe. Each sensor probe pair gave a point estimate of sapwood temperature. Paired thermistor probes were inserted into the sapwood to depths of 4, 9, 16 and 24 mm below the cambium at the Came site, and to depths of 5, 13, 23 and 35 mm at Frankfort. Each thermistor pair was connected in a Wheatstone bridge configuration and automatically zeroed before each heat pulse initiation. The logger was programmed to apply a current of 30 amperes lasting 0.5 seconds to each heater probe. HPV (u) was measured using the compensation technique (Huber and Schmidt, 1937; Swanson, 1974). The temperature rise was measured at distances X_u upstream and X_d downstream from the heater, and u was calculated as follows:

$$u = (X_u + X_d) / 2t \qquad (1)$$

where t is the time delay for the temperatures at points X_u and X_d to become equal.

Heat pulse velocities were corrected for sapwood wounding caused during the drilling procedure. Swanson and Whitfield's (1981) wound correction coefficients were used to derive corrected heat pulse velocities (u'). The correction takes the form:

$$u' = p + qu + r(u)^2 \qquad (2)$$

where p, q and r are the correction coefficients appropriate to the measured wound size, diameter of teflon probes, and probe separation distances, respectively. The size of the wound at each probe set location was measured at the end of the experiment. The four sections of the tree trunk containing the probe implantation holes were excised and re-cut longitudinally at the particular radial depth below the cambium where the thermistor was originally positioned. The exposed, fresh face was shaved smooth using a microtome to allow precise measurements of wound widths which were measured to the nearest 0.1 mm using a 7x scale loupe. These measurements were taken midway between the line heater position and both the upper and lower thermistors. A single mean wound width was calculated for each tree. The corrected heat pulse velocities were converted to sap flux (*v*) using the following equation (Marshall, 1958):

$$v = \rho_b (m_c + c_{dw}) u' \quad (3)$$

where ρ_b is dry wood density, m_c is the moisture fraction of sapwood, and c_{dw} is the specific heat of dry wood, assumed constant at 0.33 (Dunlap, 1912). In calculating wood density, the volume of a fresh sample of sapwood was determined by immersion in water and the application of Archimedes' principle. Moisture fraction was calculated as (fresh mass – dry mass) / dry mass, while basic wood density was calculated as the dry mass / volume of the freshly excised section of wood. Each of the four sap flux measurements recorded in each tree were considered to be representative of a ring of sapwood centred on the probe depth. Total sap flow was then calculated as the sum of the partial areas multiplied by their associated sap flux. Daily sap flows were calculated from hourly sap flow rates summed over the logging period between 04h30 and 19h30 each day.

7.2.5 Leaf Area

Leaf areas of the sample trees at Came were estimated from regression analysis following destructive harvesting of 16 trees representative of the range of DBH. These trees were felled at approximately three years of age and the foliage sub-sampled for fresh mass, and leaf area determination using the LI-3100 Leaf Area Meter (LI-COR Inc.). DBH values were regressed against leaf area measurements and this relationship was used to derive leaf area estimates of the sample trees. Mean leaf areas at the Frankfort site were estimated by stripping all leaves from the sample trees and estimating total area from the total mass using the relationship determined from a sub-sample of leaves.

7.2.6 Canopy Conductance

Using transpiration data from HPV measurements, daily estimates of g_c were obtained by inverting the P-M equation:

$$g_c = DL\ (g_a\ E\ \lambda\gamma\ /\ (s\ A + \rho\ C_p\ D\ g_a - \lambda\ E\ (s + \gamma))) \quad (4)$$

where:

DL = daylength (s);

g_a = boundary layer conductance (m s^{-1}). The P-M equation is not sensitive to g_a (Raupach and Finnigan, 1988; Landsberg, 1999), and this was fixed at 0.2 m s^{-1}, a representative value for forest canopies (see Kelliher *et al.*, 1993; Landsberg and Gower, 1997; Waring and Running, 1998);

E = total daily transpiration (mm) derived from the sap flow data. Sap flow data were converted to mm equivalents based on the average ground area of 6 m^2 occupied by each tree;

λ = latent heat of vaporisation of water (2450000 J kg^{-1});

γ = the psychrometric constant (0.0658 kPa $^oC^{-1}$);

s = slope of the curve relating saturated vapour pressure to temperature (0.13 kPa $^oC^{-1}$);

A = net radiation (W m^{-2}). Mean daily net radiation was estimated from daily solar radiation using a relationship recommended by Landsberg and Gower (1997):

$$A = 0.85 * \text{solar radiation} - 55\ \text{W m}^{-2} \quad (5)$$

ρ = air density (1.204 kg m^{-3});

C_p = specific heat of air at constant pressure (1010 J kg $^oC^{-1}$);

D = the vapour pressure deficit (kPa). D was averaged over daylight hours 06h00 to 18h00.

7.3 RESULTS

7.3.1 Sample Trees

Characteristics of the trees sampled for sap flow measurements are presented in Table 7.2.

Table 7.2 A summary of the salient properties of the sample trees at Came and Frankfort, recorded at the conclusion of each study. Values presented are means and (standard deviation).

Site	Came	Frankfort
Age (years)	3.0	4.0
DBH (cm)	9.2 (1.5)	14.7 (1.2)
Height (m)	9.4 (0.8)	14.7 (1.0)
Leaf area per tree (m^2)	29.6 (7.7)	62.0 (11.8)
Sapwood moisture fraction	2.01 (0.33)	1.37 (0.16)
Sapwood density ($g\ cm^{-3}$)	0.33 (0.03)	0.45 (0.04)
Wound width (mm)	2.9 (0.07)	2.8 (0.29)

7.3.2 Pre-Dawn XPP

Pre-dawn XPP measurements at Came ranged from –0.03 to –0.08 MPa over the period June to November 2001, and indicated that these trees were not water stressed at any time during the sap flow measurement period. At the Frankfort site, pre-dawn XPP data showed that the lowest potentials in the trees under plastic barely exceeded –0.70 MPa. Prevention of soil water recharge resulted in more negative water potentials compared to nearby control trees where normal soil water recharge occurred, but the greatest difference only amounted to approximately –0.30 MPa, leading to the conclusion that these trees only experienced a mild degree of stress towards the end of the monitoring period (Dye, 1996; Dye *et al*., 1997). The failure of the trees to respond to the imposed soil water deficit was attributed to their ability to abstract soil water to a depth of at least 8 m (Dye, 1996; Dye *et al*., 1997).

7.3.3 Came

Good quality HPV data were available from 15 August to 7 November 2001. Due to the very limited data record for the second sample tree at Came (owing to persistent data logger problems and frequent theft of equipment), only data from one tree were used. This single tree was representative of the remaining trees in the plot, with DBH, height and leaf area values of 10.3 cm, 10.0 m and 35.1 m^2, respectively, compared to plot-level values of 9.5 ± 3.3 cm (DBH), 9.2 ± 2.2 m (height), and 30.1 ± 17.2 m^2 (leaf area).

Estimates of g_c obtained from Equation 4 were plotted against mean daily D (Figure 7.1).

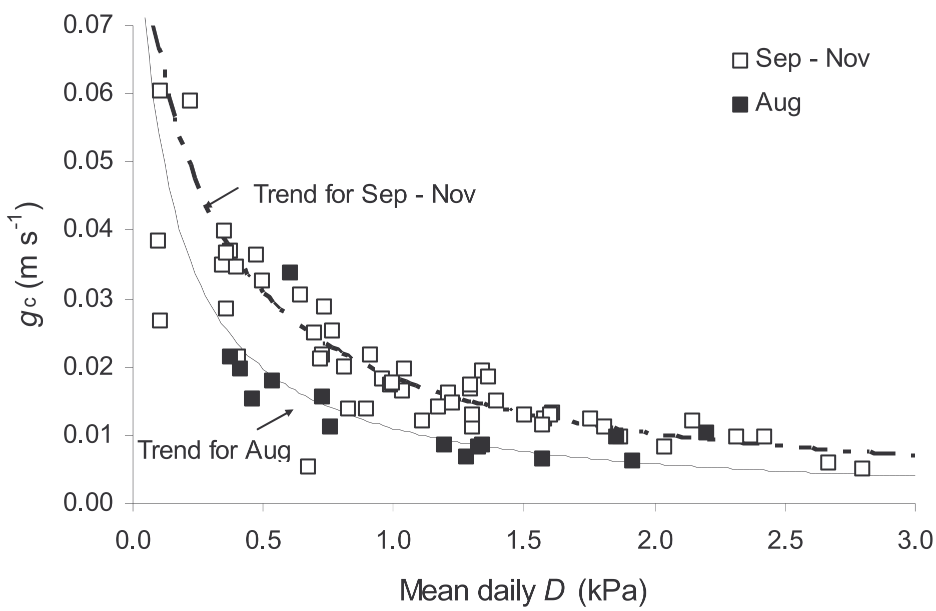

Figure 7.1 The relationship between mean daily vapour pressure deficit (D) and canopy conductance (g_c) at Came, calculated using Equation 4. A reciprocal function of the form y = 1/(a*x+b) was fitted to the September – November data (a = 43.474, b = 10.695) and the August data (a = 80.781, b = 10.337).

There is a dominant overall non-linear response to D, with g_c decreasing with increasing D. In view of the results of a previous study of *E. grandis* g_c patterns, where a distinct seasonal shift in the relationship between g_s and D occurred in early spring and late autumn (Dye and Olbrich, 1993), these data were investigated to ascertain whether such a seasonal change was observable. A clearly defined trend was found for the September – November data (open squares, Figure 7.1). Points significantly below this trend were associated with conditions of low solar radiation (< 6.3 MJ m^{-2} day^{-1}). These data points were removed before a reciprocal function was fitted to the remaining data. Data recorded during August (solid squares) were found to define a different and lower trend and a separate function was fitted to these data points. A reciprocal function of the form y = 1/(a*x+b) was fitted to the September – November data (a = 43.474, b = 10.695) and the August data (a = 80.781, b = 10.337), respectively.

We used a simple hyperbolic function to describe the relationship between solar radiation and maximum g_c (Figure 7.2), as defined by the trend lines in Figure 7.1.

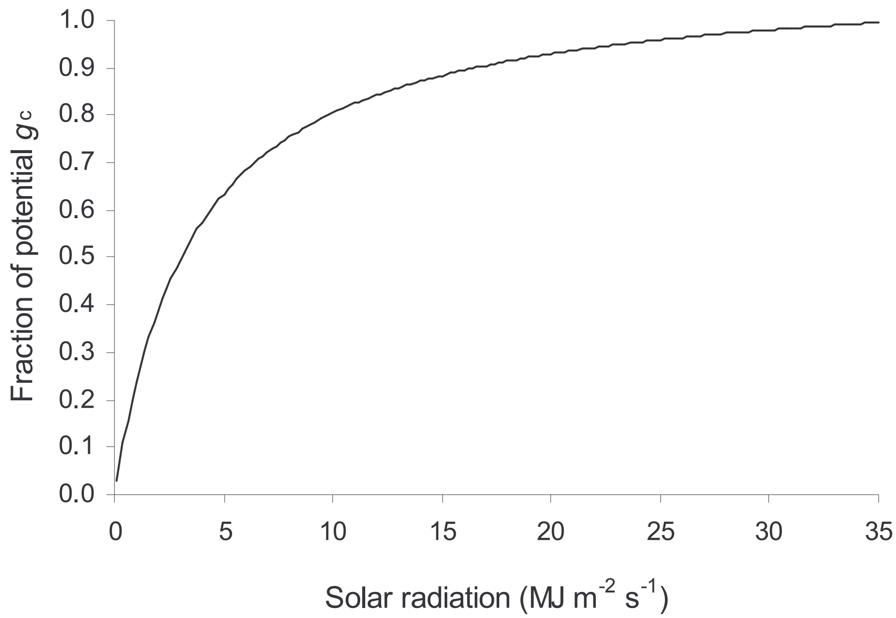

Figure 7.2 The relationship between daily solar radiation and the fraction of potential canopy conductance (g_c) at Came. The function and parameter values adopted were as follows: y = a*b*SR/(a+b*SR); a = 1.1, b = 0.3.

Parameter a was adjusted to return a value of 1 under conditions of maximum solar radiation. An optimising algorithm was used to optimise the parameter b to best fit the calculated g_c. Daily g_c was then calculated over the entire Came data record as the product of the two functions relating g_c to mean daily *D* and to total solar radiation. These estimates were compared to those calculated from the P-M equation and measured transpiration (Figure 7.3). The apparent outliers in Figure 7.3 were from data collected on days where the solar radiation did not exceed 6.3 MJ m^{-2} day^{-1}.

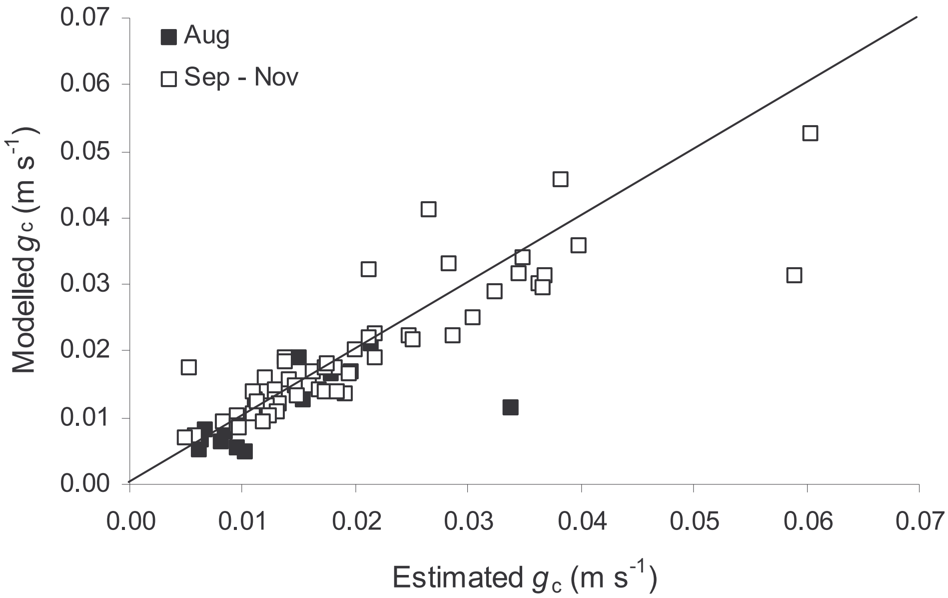

Figure 7.3 The relationship between estimated and modelled canopy conductance (g_c) for the Came site. Estimated g_c was obtained from the P-M equation and measured transpiration rates, and the modelled g_c was derived from the functions described in Figures 7.1 and 7.2.

Modelled g_c was then used to estimate daily transpiration with the P-M equation. The correspondence to measured transpiration by HPV is shown in Figure 7.4.

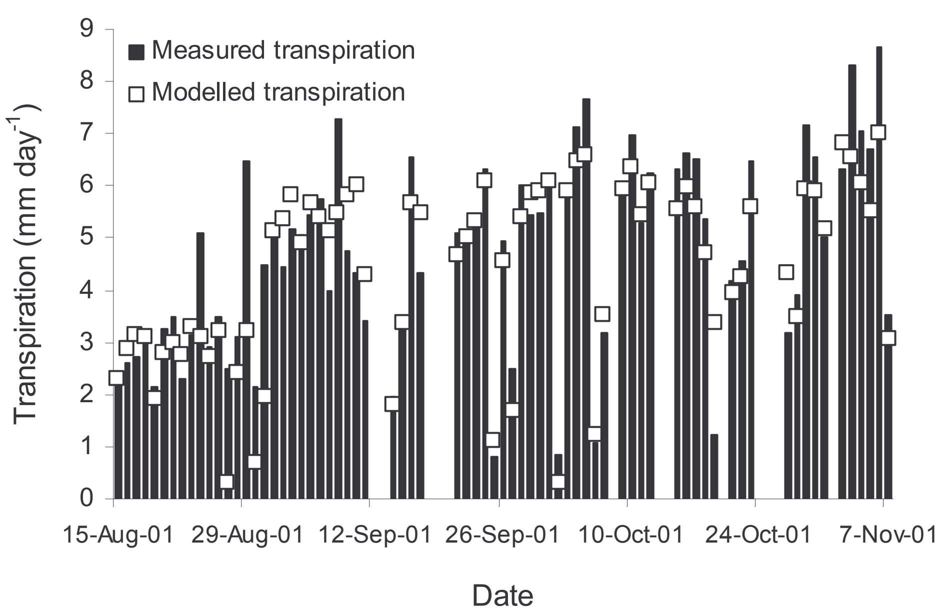

Figure 7.4 The relationship between measured and modelled daily transpiration at the Came site.

The transpiration rates determined by the two methods were well correlated (R^2 = 0.76). Days where the fit between measured and modelled transpiration was not particularly good were again related to conditions of low solar radiation.

7.3.4 Frankfort

The g_c model derived from the Came data was tested against the measured transpiration and associated weather data recorded at Frankfort. On the basis of an earlier porometer-based study (Dye and Olbrich, 1993), the summer g_c function was initially applied from September to April, while the winter function was applied from May to August. However, a better fit of the data was obtained when the summer g_c function was applied from September to May, and the winter function from June to August. This may be related to the development of mild water stress by the trees after a year of no soil water infiltration. The correlation between modelled g_c and g_c values based on the P-M equation using measured mean daily transpiration is shown in Figure 7.5.

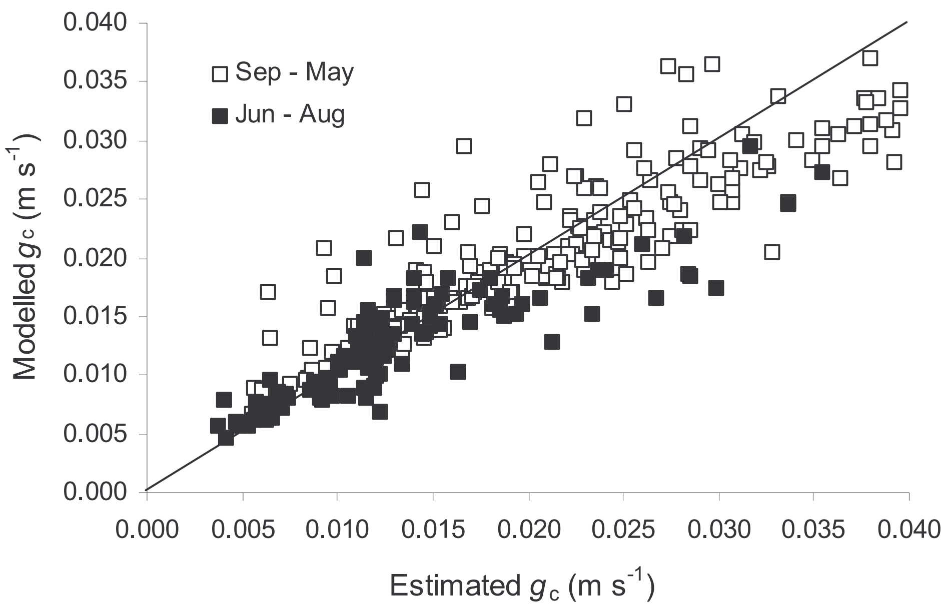

Figure 7.5 The relationship between estimated and modelled canopy conductance (g_c) for the Frankfort site. Estimated g_c was obtained from the P-M equation and measured transpiration rates, and the modelled g_c was derived from the functions described in Figures 7.1 and 7.2.

Predicted g_c was then used to estimate daily transpiration with the P-M equation. The correlation between measured and modelled daily transpiration is given in Figure 7.6.

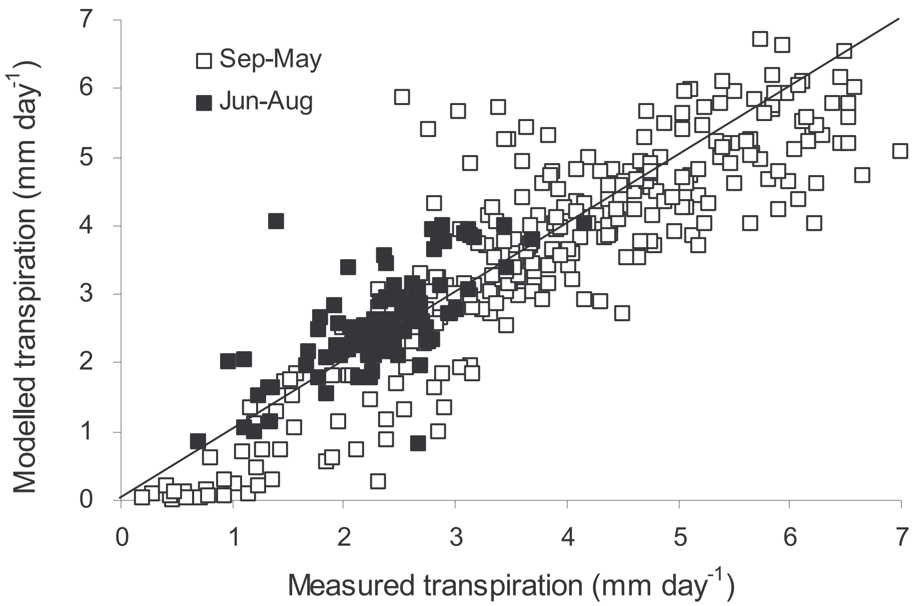

Figure 7.6 The relationship between measured and modelled daily transpiration at the Frankfort site.

7.4 DISCUSSION AND CONCLUSION

Canopy conductance was modelled as a function of *D* and solar radiation from data collected for the Came site. Many other studies point to these two environmental factors as being the major determinants of g_c and transpiration rates (Dunn and Connor, 1993; Dye and Olbrich, 1993; Green, 1993; Leuning, 1995; Kallarackal and Somen, 1997b; Granier *et al*., 2000; Soares and Almeida, 2001) where there is no soil water limitation or change in leaf area.

A similar seasonal shift in the g_c–*D* relationship, as observed in Figure 7.1, was recorded in an earlier porometer-based study of the g_s patterns in a single *E. grandis* tree (Dye and Olbrich, 1993). A seasonal shift in the relationship between *D* and g_c of *E. grandis* in Mpumalanga was also observed by Dye (1987) at the low end of the *D* range, but this could not be attributed to differences in soil moisture availability or micro-climate factors. Dye (1987) hypothesised that this pattern may be caused by substantial osmotic adjustment in the guard cells during springtime. We hypothesise that the marked changeover in the relationship between g_c and *D* at the end of August is due to a change in the osmotic potential of the leaf, and may be related to the accumulation of sugars at low water availability.

The model constructed to predict g_c from *D*, solar radiation and the season of year generated from observations at Came was tested against an independent data set collected at Frankfort. On a daily basis, a good agreement was observed between the transpiration predicted by the model and that obtained from sap flow measurements (Figure 7.6). A regression line through the data points yielded $y = 0.91x + 0.1264$ ($R^2 = 0.79$). It is evident that the model under-predicted transpiration on days of low sap flow (Figure 7.6). There were relatively few days in the Came data record on which sap flow was below 2 mm. In view of the known overestimation of low sap flows by the HPV technique when based on the compensation principle (Becker, 1998; Burgess *et al*., 2001), we believe that the model should be used in its current form until the low flow measurement problem is investigated using alternative methodology.

The cumulative transpiration measured by HPV over a one-year period at Frankfort was 1320 mm, as compared to 1226 mm estimated from modelled g_c and the P-M equation, resulting in a difference of 7.7%. Other studies have also indicated a good agreement between transpiration rates estimated by the P-M equation and those based on sap flow measurements (Edwards and Warwick, 1984; Green, 1993; David *et al*., 1997). Mean daily transpiration at the Frankfort site was 3.4 mm, with a maximum of 6.8 mm. These values lie well within the range of water use estimates cited for *E. grandis* (Dye, 1987; Dye, 1996; Myers *et al*., 1996; Dye *et al*., 1997; Kallarackal and Somen, 1997a).

The g_c model developed from the Came data and subsequent use of the P-M equation, using inputs from the Frankfort data set, provided accurate estimates of transpiration compared to sap flow rates measured by HPV. This simple model, requiring inputs of standard weather data, is useful to estimate the potential transpiration rate of a young *Eucalyptus* stand under conditions of non-limiting soil water availability.

These estimates of water use by *E. grandis* specifically address the fourth objective and associated key questions. Plantation forest growth is commonly limited by water availability and nutrient supply. Soil moisture availability is the single most important factor limiting afforestation in South Africa (Schönau and Grey, 1987). However, it is highly unlikely that irrigation of forest trees would ever be implemented on an operational scale in this country. Increases in growth could still be obtained through fertiliser application, which has been shown to be one of the most cost-effective methods of improving and maintaining the productivity of commercial plantations (Schönau, 1983; Herbert and Schönau, 1989). Fertiliser recommendations can be optimised and nutrient leaching minimised through the use of foliar diagnostic tools (Linder, 1995; Knecht and Göransson, 2004). The foliar nutrient dynamics of *E. grandis* were diagnosed to address the fifth objective and related key questions, and these results are presented in Chapter 8.

CHAPTER 8

DIAGNOSING FOLIAR NUTRIENT DYNAMICS OF *EUCALYPTUS GRANDIS* USING OPTIMAL NUTRIENT RATIOS AND THE DIAGNOSIS AND RECOMMENDATION INTEGRATED SYSTEM (DRIS)[5]

8.1 INTRODUCTION

In South Africa, fertiliser application has been shown to be one of the most effective methods of economically improving and maintaining the productivity of commercial plantations (Schönau, 1983; Herbert and Schönau, 1989). Plant analyses can be used to determine the fertility status of soils and to evaluate the effectiveness of fertiliser practices (Melsted *et al.*, 1969). Plant tissue analysis, particularly foliar analysis, is the preferred method of evaluating plant nutrient status as it provides an integrated assessment of all the factors that influence nutrition (Ulrich and Hills, 1967; Needham *et al*., 1990), such as nutrient supply, plant uptake, translocation and growth (Richards and Bevege, 1972). In South Africa, plantation eucalypts growing on well-weathered soils of low nutrient status often exhibit a healthy appearance and very rapid growth rates where the climatic conditions and soil physical characteristics are favourable (Schönau and Herbert, 1989). Consequently, foliar rather than soil analysis is considered more appropriate for determining the nutrient status of a site (Herbert, 1996). Correctly interpreted plant analyses may aid in identifying nutrient deficiencies and imbalances which may lead to a loss of potential production or decline in productivity (Melsted *et al.*, 1969).

The diagnostic techniques commonly used to assess plant nutrient status include the critical level approach (Ulrich, 1952; Ulrich and Hills, 1967; Melsted *et al.*, 1969), the diagnosis and recommendation integrated system (DRIS; Beaufils, 1971, 1973), vector analysis (Timmer and Stone, 1978), and optimum nutrient ratios (Ingestad, 1979a,b; Ericsson *et al.*, 1992; Ericsson, 1994c; Linder, 1995). The DRIS and optimum nutrient ratio techniques were adopted for use in this study.

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In the DRIS technique, any factor that potentially influences yield (e.g. soil properties, climatic conditions, management practices and plant composition) must be identified, and the relationships existing between these factors and yield must be defined (Beaufils, 1973). The established relationships are expressed as diagnostic indices which form calibrated norms, used for diagnosis and recommendation purposes (Beaufils, 1973). Despite the holistic approach of the DRIS, application of this technique is normally confined to plant and/or soil analyses only. In this system, the interrelationships between all nutrients are studied simultaneously (Schutz and de Villiers, 1987). The DRIS identifies the most limiting nutrient and ranks the order in which other nutrients may potentially limit yield, thereby incorporating the concept of nutrient balance into plant nutrition (Sumner, 1977a,b,c, 1979). The DRIS has enabled accurate diagnoses of nutritional limitations and imbalances for a variety of agricultural crops such as maize (Beaufils, 1971; Sumner, 1977c; Letzsch and Sumner, 1984; Walworth *et al*., 1988), wheat (Sumner, 1977a), soybeans (Sumner, 1977b; Beverly *et al*., 1986), sugarcane (Jones, 1981; Elwali and Gascho, 1984) and citrus (Beverly, 1987). In forestry, DRIS was initially tested on a small-scale, investigative basis only (Schutz and de Villiers, 1987), but has since been adopted on a much wider scale. The potential application of this technique has been documented for *Abies fraseri* (Hockman *et al*., 1989; Kopp and Burger, 1990; Rathfon and Burger, 1991a,b), *E. saligna* (Ward *et al*., 1985; Knight and Nicholas, 1996), *E. regnans* (Knight and Nicholas, 1996), *E. grandis* clones (Wadt, 2004), *Populus deltoides* clone (Leech and Kim, 1981; Kim and Leech, 1986), *P. radiata* (Svenson and Kimberley, 1988; Romanyà and Vallejo, 1996), *P. taeda* (Hockman and Allen, 1990; Needham *et al*., 1990), *P. patula* (Schutz, 1990), and *Tectona grandis* (Drechsel and Zech, 1994).

Ingestad (1979a,b, 1981) adopted a similar approach to the nutrient balance concept to maintain optimum nutrition in tree seedlings. In this technique, nutrients are added in fixed proportions to N found present in plants at maximum growth. Linder (1995) used this approach to detect and correct nutrient imbalances, and maintain optimal nutrient status in Norway spruce trees. Target values were set for the foliar nutrient concentrations of each element, based on results obtained from laboratory studies and long-term forest nutrition experiments, in which plant nutrient requirements were established (Linder, 1995). According to foliar analysis and predicted growth response, the quantities of nutrients to be applied were estimated in relation to the target value (Linder, 1995). Determining general optimum nutrient ratios in plants may provide a means of optimising fertilisation and minimising nutrient accumulation and leaching (Knecht and Göransson, 2004).

Some of the assumptions of the optimal nutrient ratio technique are:

- Over a wide concentration range, the proportions of elements relative to N are at least as, if not more important than the absolute nutrient concentration,
- Optimal growing conditions can only occur if all essential nutrients are present in the correct proportions, and
- Optimal nutrient element proportions are similar for all higher plants and can be defined relative to N (Linder, 1995).

The DRIS approach is also based on several assumptions, which include:

- Ratios of nutrient elements are often superior indicators of nutrient status than single elemental concentrations,
- Some nutrient ratios are more important than others,
- Maximum yields can only be attained when nutrient ratios approach an optimal value; deviations from this value result in lower growth (Jones, 1981).

It is apparent from these assumptions that the DRIS and optimal nutrient ratio techniques are fundamentally similar.

In this irrigation and fertilisation trial, an optimal foliar N concentration was defined, and target values were set for each nutrient element relative to N, according to Linder (1995). The principal objective of this study was to determine whether these optimal ratios could be fine-tuned to make them specific to *E. grandis*. This was done by generating DRIS norms from published *E. grandis* foliar nutrient concentrations and corresponding yield data. The resultant diagnoses were compared to those obtained from the optimal nutrient proportion technique of Linder (1995).

8.2 MATERIALS AND METHODS

8.2.1 Site Description and Experimental Design

A description of the site is given in Section 3.1, and the experimental design and imposed treatments are presented in Section 3.3.

8.2.2 Sampling Procedures and Foliar Nutrient Analyses

The methodology pertaining to foliar sampling and subsequent nutrient analysis is outlined in Section 3.4.2.2.

8.2.3 Diagnosis and Recommendation Integrated System

The DRIS methodology consists of (i) establishing the data bank, (ii) generating the DRIS norms, (iii) calculating the DRIS indices, and (iv) testing the norms (Schutz and de Villiers, 1987). In this study, standard DRIS procedures (see Beaufils, 1973; Sumner, 1977a; Walworth and Sumner, 1987) were largely followed; any modifications to this system are documented in the relevant sections.

8.2.3.1 Establishing the Data Bank

The data bank is comprised of foliar nutrient concentrations and corresponding yield data collected from the widest possible range of conditions (Schutz and de Villiers, 1987). The best data banks consist of a large number of sites selected at random, and comprise a considerable number of high-yield measurements (Letzsch and Sumner, 1984). The data bank in this study consisted of foliar analyses and associated growth data collected from available published information on *E. grandis* growing under field conditions. The data bank from which DRIS functions are calculated should be representative of the conditions where DRIS will be applied, e.g. if nutrient expressions should be stable with respect to age, the data bank must represent nutrient concentrations across a range of ages (Walworth and Sumner, 1987). Nutrient requirements at different ages can be diagnosed using the DRIS: In this system, nutrient elements are expressed as ratios, thus reducing the effect of the dry matter component which increases with age and therefore causes a dilution in the nutrient concentration (Sumner, 1977a,c; Walworth and Sumner, 1987).

In this irrigation and fertilisation trial, sampling for the suite of macro- and micronutrients was confined to leaves collected from the upper third of the canopy, and spanned the ages from two months to four years. To adequately represent these conditions, several criteria were used to determine whether studies would be included in the data bank: i) The data had to represent the age range from this irrigation and fertilisation trial, ii) the data were required to contain nutrient ratios, or concentrations of at least two elements (preferably N and P, or N and K), and iii) in trees older than one year, foliar sampling was restricted to leaves selected from the mid- to upper canopy. The amount of published information that could be used to establish such a data bank was much smaller than expected, and data that did not conform to these criteria were excluded. There were limited field data for juvenile growth stages, and two pot trials were included to ensure that the entire age range of this irrigation and fertilisation trial was adequately accounted for. According to Ericsson (1994c), absolute foliar concentrations are likely to decrease under natural growth conditions and during adult stages, but foliar nutrient proportions will probably remain the same. As the application of DRIS in this study was confined to nutrient ratios and did not include absolute concentrations, it was felt that the inclusion of these pot trials was justified.

Given the paucity of information on published micronutrient concentrations in *E. grandis*, the data bank was limited to the macronutrients, N, P, K, Ca and Mg. Appendix 1 contains the data bank of the foliar nutrient ratios used in the calculation of the DRIS norms. Values entered into the data bank were obtained primarily from South African studies, but also included data from Australia, Brazil and India. The foliar nutrient data were collected over a range of ages from approximately two months to seven years, and consisted of published optima and nutrient concentrations from fertiliser trials, and from a range of nutritional studies. The growth variables which corresponded to these nutrient data were tree height, diameter and volume measurements, and site index values.

The number of studies used to calculate the nutrient ratios ranged from 42 to 67, depending on the particular elements in question. Generally, more data existed for N, P and K concentrations than for Ca and Mg. In other forestry investigations, the population sizes vary considerably: 19 (*P. deltoides* clone (greenhouse standard); Leech and Kim, 1981), 30 (*P. deltoides* clone (field standard); Leech and Kim, 1981), 34 (*E. saligna*; Knight and Nicholas, 1996), 42 (*E. delegatensis*; Knight and Nicholas, 1996), 52 (*E. regnans*; Knight and Nicholas, 1996) and 147 (*P. patula*; Schutz, 1990).

8.2.4.1 Generating the DRIS norms

The data bank is usually divided into two sub-populations on the basis of yield (Sumner, 1977b). In this study, entries in the data bank that contained published optimal nutrient concentrations were automatically incorporated into the high-yielding sub-population, under the assumption that optimal nutrient status would result in high yields. The following approach was adopted for the remaining data from the fertiliser trials and nutritional studies. Firstly, no common growth variable was measured across all these studies: In some cases, various combinations of tree height, diameter, volume and site index data were presented, compared to other cases where only one response variable was measured, i.e. either tree height, volume or site index. Therefore, division of the data into the high- or low-yielding sub-population had to be based on the growth responses specific to each study. In addition, we do not have detailed knowledge of the climatic conditions, or soil physical and chemical properties for the international studies included in the data bank. Consequently, each study was investigated in isolation to ensure that the given trees were subjected to the same set of environmental conditions. It was presumed then, that the underlying factor producing the observed growth responses was nutrient-related. Within a specific study, trees which exhibited the greatest growth, and those where the growth was within 90% of this maximum value were selected as the high-yielding sub-population, under the assumption that these trees would have optimum nutrition. The remaining observations formed the low-yielding sub-population. The cut-off value used to divide the high- and low-yielding sub-populations is not critical, provided the high-yield data remain normally distributed (Walworth and Sumner, 1987). Each element is then expressed in as many ways as possible, and in as many combinations with other elements, e.g. N would be expressed as N% dry mass, as the ratio N:P, the inverse P:N, or as the product NP (Schutz and de Villiers, 1987; Walworth and Sumner, 1987). In this study, each element was expressed in combination with the other four elements, as nutrient ratios and their inverse. Nutrient concentrations and products of elements were not considered. The mean, standard deviation (SD), coefficient of variation (CV) and variance (S^2) were calculated for each form of nutrient expression in both the high- and low-yielding sub-populations (Table 8.1).

Each nutrient ratio was tested for its ability to discriminate between the two sub-populations. Discriminating ratios are identified as those with a significantly smaller variance in the high-yielding sub-population than in its low-yielding counterpart (Needham *et al*., 1990). *F*-tests were used to check for differences in the variance ratios ($S^2_{\text{low-yield}} / S^2_{\text{high-yield}}$) between these two groups. Prior to testing for variance differences, the distributions of the nutrient ratios were checked for normality to ensure a valid *F*-test could be performed. Two of the ratios (P:K and P:Mg) were significantly non-normal ($p < 0.05$). These data were successfully transformed using the natural log, and statistical analyses were conducted on these log-transformed ratios. The original (untransformed) data are presented (Table 8.1).

Table 8.1 Comparison of sample size, mean value, standard deviation (SD), coefficient of variation (CV) and variance (S^2) of nutrient ratios in the high- and low-yielding *E. grandis* sub-populations.

Form of nutrient expression	High-yielding sub-population					Low-yielding sub-population					S^2 ratio (low-yield/ high-yield)
	No. of samples	Mean value	SD	CV (%)	S^2	No. of samples	Mean value	SD	CV (%)	S^2	
P:N	22	0.08	0.02	24.7	0.0004	45	0.11	0.05	48.5	0.0030	7.00**
K:N	11	0.37	0.11	30.2	0.01	36	0.57	0.31	54.2	0.09	7.57**
Ca:N	9	0.33	0.14	43.7	0.02	33	0.54	0.24	44.9	0.06	2.86**
Mg:N	9	0.12	0.02	19.9	0.001	33	0.18	0.07	40.5	0.005	9.18**
P:K	11	0.22	0.07	31.2	0.005	36	0.23	0.10	44.8	0.010	2.24
Ca:P	9	4.67	2.07	44.4	4.28	33	4.94	2.41	48.8	5.82	1.36
P:Mg	9	0.63	0.22	34.5	0.05	33	0.71	0.34	47.6	0.11	2.39
Ca:K	9	0.90	0.42	47.2	0.18	33	1.07	0.57	53.3	0.33	1.81
Mg:K	9	0.33	0.10	29.8	0.01	33	0.35	0.14	41.5	0.02	2.16*
Ca:Mg	9	2.77	0.87	31.4	0.75	33	3.16	1.12	35.5	1.26	1.67

* and ** indicate significance at the 5% and 1% level, respectively.

Variance ratios were compared with standard *F*-table values, using a *p*-level of 0.05 to ascribe significance. In the DRIS, only one expression is used to represent each nutrient ratio; between two corresponding inverted ratios N:P and P:N, the one with the largest variance ratio between the low- and high-yielding sub-population is selected for diagnostic purposes (Walworth and Sumner, 1987). The mean values of these selected nutrient ratios for the high-yielding sub-population constitute the DRIS norms.

8.2.4.2 Calculating the DRIS indices

In the DRIS approach, the degree of nutrient imbalance is expressed in terms of DRIS indices. The indices, which sum to zero, measure the extent to which a given nutrient ratio deviates from the optimum value in a high-yielding sub-population (the established norm) (Sumner, 1977b, 1979; Escano *et al*., 1981). According to traditional DRIS methodology (Beaufils, 1973), a nutrient ratio used in the calculation of a DRIS index should have a significantly higher variance in the low-yielding compared to the high-yielding sub-population (Jones, 1981). In some investigations, however, all nutrient ratios are included in the DRIS analysis, despite non-significance of some of the associated variances (Kim and Leech, 1986; Hockman *et al*., 1989; Hockman and Allen, 1990; Needham *et al*., 1990; Shumway and Chappell, 1995). This modification of retaining all nutrient ratios is introduced since balanced, or symmetrical DRIS index equations (indices sum to zero) can only be attained if an equal number of nutrient ratios is used to calculate the indices for each individual element (Righetti *et al*., 1988; Rathfon and Burger, 1991b). In this study, the nutrient expressions for P:N, K:N, Ca:N, Mg:N, P:K, Ca:P, P:Mg, Ca:K, Mg:K and Ca:Mg had the largest variance ratios between the two sub-populations and were therefore selected for diagnostic purposes (Table 8.1). Although the *F*-tests for P:K, Ca:P, P:Mg, Ca:K and Ca:Mg were not significant, these nutrient ratios were also retained as norms in the development of the DRIS indices to provide a more balanced diagnosis of the nutrient status.

The DRIS index equations were calculated using the following formula for hypothetical nutrients A through N:

$$\text{A index} = [f(A/B) + f(A/C) - f(D/A) \ldots + f(A/N)]/z \quad (1)$$

where

$$f(A/B) = 100\,[(A/B)/(a/b) - 1](k/CV) \text{ if } A/B \geq a/b \quad (2)$$

or

$$f(A/B) = 100\,[1 - (a/b)/(A/B)](k/CV) \text{ if } A/B < a/b \quad (3)$$

In these equations, *f* is the functional relationship between the sample being diagnosed and the optimal value, or norm, for a particular nutrient ratio (Needham *et al*., 1990). A/B is the ratio of the two elements in the sample under investigation and a/b is the norm for that particular ratio. The CV is the coefficient of variation of the norm, and k is a constant that determines the magnitude of the indices, and can be ascribed any convenient value (Beaufils, 1973). A value of 10 was selected for k in this study (see Beaufils, 1973). The factor 100 is introduced because the standard deviations have been multiplied by (100/mean) to obtain the CVs (Black, 1993). In these DRIS equations, the deviation of each nutrient ratio from its optimum is weighted by the inverse of the associated CV (Walworth and Sumner, 1987). The signs of the functions in the DRIS indices are determined by the position of the element for which the index is being calculated, e.g. if the element is the numerator in a particular ratio, the function is positive, if the denominator, the function becomes negative (Schutz and de Villiers, 1987). The divisor, z, represents the number of functions comprising the nutrient index (Walworth and Sumner, 1987). Values for the other functions, such as $f(A/C)$, $f(D/A)$, etc., are calculated in the same way as $f(A/B)$, using the appropriate norms and CVs (Walworth and Sumner, 1987).

In this study, the DRIS indices were derived using Equations 4 through 8:

$$\text{N index} = [-f(P/N) - f(K/N) - f(Ca/N) - f(Mg/N)]/4 \quad (4)$$

$$\text{P index} = [f(P/N) + f(P/K) - f(Ca/P) + f(P/Mg)]/4 \quad (5)$$

$$\text{K index} = [f(K/N) - f(P/K) - f(Ca/K) - f(Mg/K)]/4 \quad (6)$$

$$\text{Ca index} = [f(Ca/N) + f(Ca/P) + f(Ca/K) + f(Ca/Mg)]/4 \quad (7)$$

$$\text{Mg index} = [f(Mg/N) - f(P/Mg) + f(Mg/K) - f(Ca/Mg)]/4 \quad (8)$$

The DRIS indices have positive and negative values which sum to zero as they measure the relative balance between the nutrients (Sumner, 1977a,b). Negative indices indicate relative nutrient deficiencies, and positive indices, relative sufficiency or excess (Walworth and Sumner, 1987). Sumner (1990) emphasised that as the DRIS indices only rank nutrients in relative order, it cannot automatically be inferred that a particular nutrient is deficient, but only that it is insufficient relative to the other nutrients. The relative order and magnitude of the indices are important for diagnostic purposes (Beaufils, 1973).

8.2.4.3 Testing the DRIS norms

DRIS norms must be tested against independent data to ensure they are capable of providing diagnoses and recommendations which are likely to increase yield (Sumner, 1977a,b). When testing DRIS norms, diagnoses are usually conducted on field- or greenhouse-grown plants from factorially-designed fertiliser trials (Walworth and Sumner, 1987). Foliar nutrient data from a given treatment (usually the control plot) are used to make a diagnosis of the most limiting nutrient. The treatment combination which satisfies the recommendation made from the original diagnosis is selected, and the yield response data are compared. A yield increase is scored as a success, and a yield decrease as a failure (Letzsch and Sumner, 1984).

8.3 RESULTS AND DISCUSSION

The mean values and associated statistical parameters for each of the nutrient expressions are presented for the high- and low-yielding sub-populations (Table 8.1). In the DRIS approach, it is assumed that some nutrient ratios are more important than others. The important nutrient ratios are those in which the variance of the low-yielding sub-population is significantly higher than the high-yielding sub-population (Jones, 1981). According to this assumption, the ratios of P:N, K:N, Ca:N, Mg:N and Mg:K were more important than the other nutrient expressions in this study. The more significant a particular variance ratio, the greater the sensitivity of the DRIS indices for the corresponding elements (Kim and Leech, 1986). In this study, the highest significant variance ratios were observed for the elements relative to N. It is interesting that the optimal nutrient ratio technique uses elemental proportions defined in relation to N, and these same forms of nutrient expression were identified by the DRIS as the most important nutrient ratios.

These important DRIS norms were compared to the target values used by Linder (1995) to maintain optimal nutrient status in Norway spruce (Table 8.2).

Table 8.2 Foliar nutrient ratios for elements relative to N, considered optimal by Linder (1995), compared to *E. grandis* DRIS norms derived from published data. All ratios are presented on a mass basis (as a % of N), with N = 100.

Nutrient ratio	Optimal value[1]	DRIS norm[2]
P:N	10.0	8.3
K:N	35.0	37.1
Ca:N	2.5	32.7
Mg:N	4.0	11.8

[1] After Linder (1995); ratios used as target values to maintain optimal nutrient status in Norway spruce.
[2] Optimum values from the high-yielding sub-population.

The P:N and K:N values were in agreement, but the DRIS norm for Ca relative to N was an order of magnitude higher, and that for Mg, almost three times greater than the target level recommended by Linder (1995) (Table 8.2). Calcium and Mg are often taken up in excess of growth requirements (Ericsson, 1994a). A similar trend was observed by Knecht and Göransson (2004), who calculated foliar nutrient ratios from published data on a wide range of plant species. These authors found that the ratios of K, Ca and Mg to N were, in most cases, higher than the optimum values derived from laboratory experiments, confirming that plants are generally limited by either N or P. A comparison of these nutrient ratios indicated that excessive uptake occurred in the order Ca > Mg > K, and Knecht and Göransson (2004) suggested that Ca is taken up in amounts corresponding to availability rather than plant demand. In Norway spruce trees, foliar Ca levels were an order of magnitude higher than the target value during autumn sampling periods (Linder, 1995), and in a nutrient optimisation trial on *E. globulus* in Portugal, nutrient uptake in excess of growth requirement was observed particularly for Ca (Pereira *et al*., 1994).

Evidence of similar optimum nutrient ratios across a wide range of plant species has been presented by Ingestad (1979b, 1987) and Knecht and Göransson (2004). The foliar elemental proportions in *E. globulus* seedlings grown under non-limiting nutrient conditions were 100 N: 10.5 P: 37 K: 10 Ca: 9 Mg (Ericsson, 1994c). The ratios of K and Mg to N are similar to the DRIS norms generated for *E. grandis* (Table 8.2). However, the DRIS norm for P was lower than the optimum value measured in *E. globulus*, whereas the Ca norm was three times higher. Ericsson (1994c) established that the uptake of P under non-limiting nutrient conditions could be decreased to a value of 7.9 without affecting the maximum relative growth rate of the *E. globulus* seedlings. The lowest nutrient ratios required to sustain maximum growth of birch seedlings were derived from laboratory experiments as 100 N: 8 P: 30 K: 2 Ca: 4 Mg (Knecht and Göransson, 2004). Besides the probable luxury consumption of Ca and Mg evident in the DRIS norms, the P:N and K:N ratios calculated for *E. grandis* agree closely with other species. It appears that the revised target value of 33 for K relative to N is reasonable, but the P:N ratio should not be reduced to less than 8. Investigations by Ingestad (1979b) revealed that variations around the optimum nutrient proportions can be tolerated without a reduction in growth. However, we have no evidence to indicate how wide the variation around an optimum value might be before a growth reduction occurs.

Encouraged by the generally good agreement between optimal foliar nutrient ratios for *E. grandis* and other species, the DRIS norms were applied to data from the irrigation and fertilisation trial. This trial could not be used to adequately test the generated DRIS norms, as this experiment was not designed as a factorial fertiliser trial, and the computed DRIS indices did not serve as a guide for the application of fertiliser. However, the potential application of this system was shown by using the DRIS indices to i) evaluate the state of nutrient balance in the trees, immediately after planting and at four years of age, and ii) to demonstrate the changes in relative nutrient status following fertiliser application.

A modification in the calculation of the DRIS indices was proposed, based on the relatively high Ca and Mg norms derived from published *E. grandis* data, and on the following discussion. Knecht and Göransson (2004) plotted the distributions of foliar nutrient concentrations relative to N using published data on a range of plant species. The narrowest distributions were observed for P, closely followed by K, but with considerable variability in Mg and particularly Ca. Although laboratory studies have indicated that all elements can be taken up in excess of requirements for growth, plants also have the ability to down-regulate uptake to prevent nutrient accumulation at toxic levels (Knecht and Göransson, 2004). Distributions of foliar P, K, Ca and Mg versus N suggest that pronounced down-regulation may exist for N, P and K, less so for Mg, and almost non-existent for Ca (Knecht and Göransson, 2004). Therefore, we proposed the use of a discrete norm value for nutrient ratios containing combinations of N, P or K, but introduced a norm range into the DRIS indices for all ratios that incorporated Ca or Mg. These elements were considered to be in optimum balance if the ratio of their concentrations in a sample under diagnosis lay within the range given by the mean value plus or minus the SD of that ratio in the high-yielding sub-population (Elwali and Gascho, 1984). The norm range was delineated by subtracting one SD from the mean value of the norm for the lower bound, and adding one SD for the upper bound (Rathfon and Burger, 1991a). The modified norm for Ca:N, for example, ranged from 0.18 (lower bound) to 0.47 (upper bound). Using this norm range,

$$f(\text{Ca/N}) = 100\ [(\text{Ca/N})/0.47 - 1](\text{k/CV}) \qquad (9)$$

if Ca/N ≥ 0.47 (upper bound of the norm range)

or

$$f(\text{Ca/N}) = 100\ [1 - 0.18/(\text{Ca/N})](\text{k/CV}) \qquad (10)$$

if Ca/N < 0.18 (lower bound of the norm range)

We believe that calculating the indices using the above modification would minimise the chances of erroneously declaring severe imbalances of Ca or Mg, particularly where accumulation of these elements occurred at rates that exceeded the requirements for maximum growth.

The NBI was used to evaluate the state of nutrient balance in each of the treatments, immediately after planting and at four years of age (Table 8.3). The NBI is calculated as the sum of the absolute values of all the DRIS indices and can be used as a measure of total nutritional balance for the elements examined (Elwali and Gascho, 1984). The higher the NBI value, the greater the nutritional imbalance.

Immediately after planting, the DRIS indices indicated a severe nutrient imbalance, which was reflected in the high NBI value of 90 (Table 8.3). The DRIS analysis revealed N as the most limiting element, compared to P, which was present in relative excess. This diagnosis was confirmed by the low N (1.20%) and high P (0.34%) concentrations. According to Boardman *et al*. (1997), marginal N concentrations in juvenile *E. grandis* trees range from 1.48 – 1.80%, and high P values are those in excess of 0.30%.

Table 8.3 Foliar nutrient concentrations and DRIS indices showing the order of nutrient requirement and nutritional balance index (NBI) in *E. grandis* trees, immediately after planting, and at four years of age.

Treatment[1]	Nutrient concentrations (%)					DRIS indices					Order of nutrient requirement	NBI
	N	P	K	Ca	Mg	N	P	K	Ca	Mg		
At establishment	1.20	0.34	0.96	0.76	0.29	-45	33	5	1	6	N > Ca > K > Mg > P	90
C	2.41	0.15	0.66	0.59	0.24	6	-3	-3	0	0	P = K > Ca = Mg > N	12
I	2.34	0.15	0.66	0.53	0.24	6	-3	-3	0	0	P = K > Ca = Mg > N	11
F	2.37	0.16	0.71	0.77	0.23	5	-3	-2	0	0	P > K > Ca = Mg > N	9
IF	2.38	0.16	0.63	0.66	0.23	6	-2	-4	0	0	K > P > Ca = Mg > N	12

[1] At establishment refers to analyses conducted on trees immediately after planting and before the initiation of treatments. C = control, I = irrigated, F = fertilised and IF = irrigated and fertilised trees aged four years.

The foliar nutrient concentrations at four years of age were very similar across all the treatments (Table 8.3). The N concentration closely approached the optimal value (2.30%), whereas the levels of P and K were considered limiting, and the ratios of Ca and Mg to N indicated uptake of these elements in excess of the requirements for growth when compared to Linder's (1995) target values (Table 8.2). The foliar concentrations of Mn, Fe, Zn, Cu and B relative to N exceeded the target values and it was concluded that these elements were not limiting (data not shown). At this age, the NBI value across all treatments had decreased, and revealed a more balanced nutrient status than that measured immediately after planting.

According to the DRIS indices, N was relatively sufficient in all treatments, compared to P and K which appeared limiting to growth. As the nutrient ratios containing Ca and Mg lay within the defined norm ranges, these elements were considered to be in optimum balance, as indicated by the zero value for these indices. High yields can only be obtained when the sum of the indices is small (where nutrients are balanced), however, even under balanced nutrition, low yields may still occur if environmental conditions are unfavourable (Walworth and Sumner, 1987). The stand characteristics at four years are presented in Table 5.1. The significant effect of irrigation on tree growth at this age indicated that on this relatively fertile site, the trees were limited more by water availability than nutrient supply. This may explain the relatively poorer growth of the F trees in spite of a more balanced nutrient status, as suggested by the lower NBI value (Table 8.3).

The DRIS is able to rank nutrients in order of requirement, and identified K as potentially more limiting to growth than P in the IF treatment at age four years (Table 8.3). The lowest K concentration was measured in these trees (0.63%), and this was attributed to a dilution effect caused by an increasing leaf biomass (Jarrell and Beverly, 1981). In the IF treatment, the K index contributed to the relatively higher NBI value. Potentially greater responses to increased water availability may have occurred in the IF treatment had optimal nutrient status been reached.

The changes in relative nutrient status following fertiliser application at two different ages are presented in Table 8.4. These specific time periods were chosen to emphasise the importance of using accurate DRIS norms and correctly interpreting the DRIS indices. Rather than discussing each diagnosis in detail, only some of the indices have been selected and interpreted to show the potential application of the DRIS technique.

The DRIS indices identified Mg as the nutrient most limiting to growth in the F and IF treatments at 1.3 years, followed by K, P, Ca and N (Table 8.4). A similar diagnosis was made when comparing the foliar N concentration with the target value of 2.3%, and the P, K and Ca to N ratios with Linder’s (1995) optimal values (see Table 8.2). The Mg:N ratio, however, exceeded the target value and this element was not considered limiting according to the optimal nutrient ratio technique. A similar diagnosis was made at 1.8 years. It is clear that the norm range introduced into the DRIS indices for all ratios containing Mg was not wide enough to adequately diagnose the Mg status in this study. This analysis highlights the importance of using accurate DRIS norms in the application of this system, as an imprecise norm could result in an incorrect diagnosis.

Table 8.4 Effect of fertiliser application on the relative nutrient status of fertilised (F and IF) *E. grandis* trees. The foliar N concentration and ratios of each element to N are presented. DRIS indices indicate the order of nutrient requirement.

Tree age (years)	Foliar N concentration (%) and nutrient ratios					DRIS indices					Order of nutrient requirement
	N	P:N	K:N	Ca:N	Mg:N	N	P	K	Ca	Mg	
					F						
1.3	3.1	5.4	22.0	31.5	5.2	21	-3	-7	6	-17	Mg > K > P > Ca > N
1.8	3.5	5.8	25.8	55.8	7.6	11	-6	-7	13	-11	Mg > K > P > N > Ca
2.8	2.3	6.9	23.8	42.5	8.4	9	0	-9	4	-4	K > Mg > P > Ca > N
3.1	2.6	7.3	32.7	34.6	9.0	3	-1	-1	0	-1	P = K = Mg > Ca > N
					IF						
1.3	2.9	5.8	25.4	32.1	4.9	20	-1	-3	6	-22	Mg > K > P > Ca > N
1.8	3.9	6.1	31.4	29.0	6.3	11	-4	0	2	-10	Mg > P > K > Ca > N
2.8	2.3	6.6	31.8	55.0	10.9	3	-4	-3	8	-3	P > K = Mg > N > Ca
3.1	2.6	7.6	33.7	35.4	9.7	2	-1	-1	0	0	P = K > Ca = Mg > N

The application of fertiliser at 1.6 years (see Table 3.4) was not sufficient to meet the demand for P and K in the F treatment, as the indices for these elements were still negative at 1.8 years. In the IF treatment, P was still relatively deficient, but K was considered optimal in relation to the other elements.

At age 2.8 years, the P and K ratios to N were lower than the target levels, and fertiliser was applied at 3.0 years (Table 3.4). The application of these elements increased their ratios at 3.1 years; this was reflected in the relatively lower values of the DRIS indices for P (IF treatment) and K (F and IF treatment) (Table 8.4). The zero DRIS index for P in the F treatment at 2.8 years suggested an optimal P status. However, it cannot automatically be inferred that an element is at an optimal level, but only that it is optimal relative to the other elements under diagnosis (Sumner, 1990). In this instance, the foliar P level in the F treatment may have been at an optimal status relative to the other elements, but the P:N ratio of 6.9 was below the target level and indicated that P was in fact potentially limiting to growth. The importance of a correct interpretation of the DRIS indices was stressed by Beverly *et al*. (1986), who stated that these values represent a relative, and not an absolute nutrient status. For this reason, it would be beneficial to combine the DRIS approach with the optimal ratio technique to aid interpretation of the DRIS indices and to rank the nutrients in order of requirement.

8.4 CONCLUSIONS

The DRIS norms generated from published *E. grandis* data for P and K relative to N corresponded to the target levels recommended by Linder (1995) for optimal growth. The Ca:N and Mg:N ratios, however, were much higher, indicating possible luxury consumption of these elements. The DRIS norms were used to evaluate the nutrient balance in the C, I, F and IF treatments, and to demonstrate changes in the relative nutrient status following fertiliser application. In most cases, the diagnosis made using the DRIS indices was confirmed with the optimal ratio approach. The DRIS appears useful for diagnosing the nutrient status, provided accurate DRIS norms are used and indices are interpreted correctly.

The precision of the DRIS norms can be increased by expanding the data bank (Jones, 1981; Schutz and de Villiers, 1987), using nutrient ratios derived from experimental data rather than published values (Escano *et al*., 1981), and including micronutrients in the diagnosis (Svenson and Kimberley, 1988; Rathfon and Burger, 1991a). Furthermore, factorial fertilisation experiments should be established to enable appropriate testing of the DRIS norms. Until such time that this type of research has been successfully completed for *E. grandis*, we suggest maintaining the foliar P:N ratio at a level of at least 8, and the other elements in the proportions recommended by Linder (1995) as optimal, and where pronounced luxury consumption is avoided.

Appropriate data were collected to address the specific objectives stated for each component of the study. The following discussion chapter focuses on the influence of water and nutrient availability on tree-water relations, nutrient dynamics and acquisition, and carbon allocation in *E. grandis* trees.

CHAPTER 9

DISCUSSION

Forest plantations can be successfully managed in both an environmentally and economically sustainable manner provided the way in which water and nutrient availability interact with prevailing climatic conditions to determine potential productivity can be understood (Albaugh *et al.*, 1998). Biomass production is usually limited by low availability of growth resources, which restrict leaf area development and light interception, and lower the efficiency of radiation conversion (Linder *et al.*, 1985; Rook, 1985; Linder *et al.*, 1987). Timber yields can be improved by increasing productivity or by increasing the proportion of biomass allocated to the harvested stem, either through genetic selection or silviculture (Linder and Rook, 1984). Silvicultural operations such as irrigation, fertilisation and vegetation control can increase soil water availability and nutrient supply to the trees, producing a higher *L* and increasing stand productivity (Beadle, 1997).

The following discussion will highlight the key findings from the trial established in the KwaZulu-Natal Midlands to determine the climatic and nutritional controls on the growth of *E. grandis* under a given set of environmental conditions. The purpose of acquiring these results was to demonstrate potential forest yields by adjusting water and nutrient supply to uptake requirements. The yield potential of *E. grandis* trees at this site could not be demonstrated, owing to a host of constraints which arose primarily from poor establishment and management practices. Given the collective effects of poor seedling quality, inadequate vegetation control, insufficient irrigation, late fertiliser application and damage from animals, it is clear that maximum growth at this site could not be achieved, even with the combined application of water and nutrients (IF treatment). Consequently, the experiment served to provide comparisons between the different treatments rather than demonstrating maximum potential growth under optimal water availability and nutrient supply. This discussion is centred on the influence of water and nutrient availability on tree-water relations, nutrient dynamics and acquisition, and biomass production and allocation. The effects of the various constraints experienced at the site are highlighted.

9.1 TREE-WATER RELATIONS

Soil water availability is the most common limitation to growth and water use in South African forestry plantations. Accurate predictions of the maximum amount of water that can be transpired by eucalypt trees would provide a useful reference against which to compare evapotranspiration rates at any *Eucalyptus* site to estimate the degree of reduction in potential water use caused by soil water deficits. In addition, it is possible that industrial waste water may be applied as irrigation water to eucalypts and it is important to predict the maximum transpiration rates of these plantations in an attempt to dispose of this contaminated water.

Daily sap flow data were recorded in a single tree from an irrigated (I) plot and used to estimate mean daily g_c. Analysis of daily and seasonal variation in conductance confirmed that solar radiation and *D* are the dominant factors reducing g_c below potential values, when soil water availability is high. A seasonal change in the relationship between g_c and *D* was observed. A simple g_c model based on these data and the season of year was then used with the P-M equation to predict daily transpiration rates by *E. grandis* trees at a second site situated in Mpumalanga. These model predictions were compared to a mean daily sap flow rate recorded in four sample trees over a full year. Transpiration estimated using the P-M equation and g_c model agreed well with the observed daily sap flow (R^2 = 0.79). The total observed annual sap flow at the Mpumalanga site was equivalent to 1320 mm, with a mean daily rate of 46 ℓ $tree^{-1}$. The corresponding modelled annual sap flow was 1226 mm.

Pre-dawn XPP was measured four times over the period June 2001 – June 2002. The pressure potentials in the irrigated (I and IF) treatments were compared to those without irrigation (C and F) over the two winter periods and during spring/summer to assess the relative water status of these trees. The pre-dawn XPP in irrigated trees during the spring/summer sampling period ranged from –0.03 to –0.08 MPa, compared to –0.04 to –0.09 MPa in trees that did not receive additional water. Over the two winter periods, the pre-dawn values measured in the irrigated trees ranged from –0.05 to –0.50 MPa, compared to –0.54 to –0.73 MPa in non-irrigated trees. The low XPP values measured in the irrigated trees during winter were caused by pump failure, with the result that no irrigation water could be applied.

At a site in Mpumalanga supporting three-year-old *E. grandis*, the pre-dawn XPP of trees experiencing normal soil water recharge ranged from approximately –0.16 in summer to –0.66 MPa in winter (Dye, 1996). In trees subjected to a progressive soil water deficit, XPP ranged from –0.36 to –0.74 MPa (Dye, 1996). Dye (1996) concluded that these trees were not severely water-stressed. In comparison to these data, the trees in this irrigation and fertilisation trial did not experience extreme water stress during the particular sampling periods, but the non-irrigated trees had a relatively lower water status, an effect that was very highly significant ($p < 0.001$) during winter 2001 (–0.05 MPa in irrigated versus –0.73 MPa in non-irrigated trees).

9.2 GROWTH RESPONSES, NUTRIENT ACQUISITION AND CARBON ALLOCATION

Biomass and N and P pools were quantified at age four years to provide a mid-rotation value of the N and P contents contained in the above- and below-ground tree components. Increased water availability had a more pronounced effect on growth and biomass accumulation compared to fertiliser addition. Irrigation improved tree height and significantly increased DBH, BA and standing volume. The effect of irrigation on biomass accumulated in the foliage, live branch, bark, stem, total above-ground and total above- and below-ground fractions was significant. The addition of fertiliser also produced a significant foliar mass response, but the effect was not as marked as that produced by irrigation.

The dry matter distribution between roots and shoots of forest species is determined by a range of factors including site quality (Santantonio, 1989), tree age and season (Ericsson *et al.*, 1996), mineral nutrition (Linder and Rook, 1984; Ågren and Ingestad, 1987; Ericsson, 1994a), water availability (Axelsson and Axelsson, 1986; Fabião *et al.*, 1995) and silviculture (Misra *et al.*, 1998a). Increased resource availability can increase stem growth through higher photosynthetic rates, canopy expansion, or a change in the allocation of photosynthates (Binkley, 1986). Shifts in carbon allocation patterns in response to increased growth resources have been documented for fertilisation (Cromer *et al.*, 1993b; Keith *et al.*, 1997; Bergh *et al.*, 1999) and irrigation (Pereira *et al.*, 1989; Madeira and Pereira, 1990/91; Pereira *et al.*, 1996; Hunter, 2001; Stape, 2002; Stape *et al.*, 2004a). In this trial, significantly more above-ground biomass was allocated to the stems of irrigated (I and IF) trees. A weakly significant fertiliser effect was evident, which resulted in a lower root:shoot ratio than in unfertilised (C and I) trees.

Irrigated (I and IF) trees accumulated more N and P in the above- and below-ground biomass components than in non-irrigated trees. The highest N and P contents in the stem were measured in the I treatment, driven by the biomass accumulation in these trees, in combination with the high concentration of these elements in this biomass component. An increased nutrient uptake as a result of irrigation has been documented by Axelsson and Axelsson (1986), Pereira *et al.* (1989) and Hunter (2001). Pereira *et al.* (1989) suggested that increased soil moisture in irrigated *E. globulus* plots in Portugal increased the amount of available nutrients and the volume of soil explored by the roots.

9.3 APPLICATION OF FOREST PRODUCTIVITY MODELS

Plant response to site factors that are manipulated (e.g. fertility) have their initial effects at the physiological level (Johnsen *et al.*, 2001). Process-based models simulate stand productivity in terms of the underlying physiological processes that govern growth, and the way trees are influenced by the physical conditions which they are subjected to, and with which they interact (Landsberg and Gower, 1997; Landsberg *et al.*, 2001). Process-based models can be used to explore the extent to which various environmental factors interact to limit production and to provide predictions about biomass partitioning (Battaglia and Sands, 1997). However, it is important to build user confidence in the accuracy of a model, and it is therefore essential that any model be validated with accurate measurements.

The 3-PG model was validated in this study using observed L, and foliage and above-ground woody biomass, and then used to predict stand volume. This study builds on the earlier work conducted by Gush (1999), Dye (2001), Esprey and Smith (2002) and Dye *et al.* (2004), who demonstrated the potential use of 3-PG as a tool for modelling South African forest productivity. The novel contribution from this trial is the application of 3-PG to trees subjected to irrigation and fertilisation treatments, which could aid in scenario analysis and planning, and the development of fertiliser recommendations.

The model was initialised at age two and simulations were run for a two-year period using a parameter set developed for *E. grandis* for the summer rainfall region of South Africa. Evaluation of the 3-PG model outputs against field measurements indicated a generally good correlation for growth data across all treatments. At four years, the model-predicted *L* over all treatments ranged from 3.8 to 5.1, similar to the observed range of 4.3 to 4.9. Leaf area index determines radiation interception, which drives carbon assimilation and stand growth, as well as transpiration rates (Landsberg *et al.*, 2001). It is therefore essential to ensure that maximum *L* produced by a stand, and the time course of this variable are consistent with observations (Landsberg *et al.*, 2001). Unfortunately, only two data points for each treatment could be used to compare observed and simulated *L* values, but the close agreement between these increases user confidence that the 3-PG model predictions of growth and biomass data are accurate for the correct reasons.

9.4 NUTRIENT DYNAMICS

Nutrition influences canopy quantum efficiency and the allocation of carbohydrates between different tree components (Landsberg *et al.*, 2001). The dynamic nature of the underlying relationships between nutrition and growth was addressed by Ingestad (1982, 1991): Nutrient uptake is determined by the growth rate of the plant and the nutrient concentration and availability in the soil. The nutritional status of a site can be improved through silvicultural operations such as site preparation and fertilisation. In South Africa, fertiliser application is one of the most cost-effective methods of improving and maintaining the productivity of commercial plantations (Schönau, 1983; Herbert and Schönau, 1989).

The prerequisites for consistent and optimal benefits from fertilisation at the time of establishment are the use of vigorous nursery stock and thorough weed control (ICFR, 2000). In this trial, fertiliser was applied four months after trial establishment; the current recommendation is an application as soon as possible (within five weeks) after planting (ICFR, 2000). In addition, some of the seedlings were of a poor and variable quality, and vegetation control was inadequate. Thorough vegetation control is essential as weeds respond very quickly to fertilisers, thereby reducing availability to the tree, and increasing competition for light and soil water (Schönau and Herbert, 1989). The effectiveness of fertiliser application is also determined by soil water availability (Gonçalves *et al*., 1997), as nutrients cannot be absorbed from dry soils (Landsberg, 1986a). Responses to fertilisation include rapid colonisation of the soil by the roots, improved survival, rapid canopy closure and suppression of weeds, a more uniform stand and increased yields at harvesting (Herbert, 1985).

A higher rate of production occurs on those stands where canopy closure is rapidly obtained (Ericsson *et al.*, 1996). This is related to the development of leaf area and an increase in light interception, which directly increases production (Binkley *et al*., 1997). In this study, the potential response to increased nutrient supply was not realised, owing to the late fertiliser application in combination with the poor seedling quality and inadequate vegetation control. Evidence of this was shown by the time of canopy closure in this trial which occurred at a stand age of approximately 2.2 years (across all treatments), compared to 1.3 years which is the norm for *E. grandis* plantations in the KwaZulu-Natal Midlands.

The nutrient status at a site can be assessed through soil or plant tissue analyses. In South Africa, foliar rather than soil analysis is considered the most appropriate technique to assess nutrient status, as plantation eucalypts often exhibit extremely high growth rates on well-weathered, nutrient-poor soils (Schönau and Herbert, 1989; Herbert, 1996). Foliar analysis can be used to recommend fertiliser application rates (Ericsson, 1994c), and to evaluate the effectiveness of these practices (Melsted *et al.*, 1969; Herbert, 1992, 1996). According to Schönau (1982) and Schönau and Herbert (1983), the foliar ratios between N, P, K, Ca and Mg give a clearer and more direct indication of the nutrient status and fertiliser requirements of eucalypts than the concentrations of these individual elements. Determining general optimum nutrient ratios in plants may provide a means of optimising fertilisation and minimising nutrient accumulation and leaching (Knecht and Göransson, 2004). The optimum nutrient ratios present in plants at maximum growth are similar across a wide range of species (Ingestad, 1979b, 1981, 1987; Knecht and Göransson, 2004). According to Ericsson *et al*. (1992), these similarities are not surprising considering that all plants share the same basic physiological processes such as photosynthesis, respiration, cell division and the production of associated enzymes.

Foliar analysis was used in this trial as a tool to diagnose the nutrient status of the trees, and as a basis for fertiliser recommendations. An optimal foliar N status was defined, and target values were set for each nutrient element relative to N. The target values were based on recommendations made by Linder (1995) for optimum growth of Norway spruce, and on documented foliar levels from South African literature. The DRIS technique was used to generate optimal foliar concentrations specifically for *E. grandis*, to determine whether the target values recommended by Linder (1995) could be refined for this species. The optimal ratios of P and K to N, generated using the DRIS, were in close agreement with recommended optima (Linder, 1995), but the high Ca:N and Mg:N values indicated uptake of these elements in excess of growth requirements. The foliar nutrient status of this trial was diagnosed using the DRIS technique and the target values recommended by Linder (1995). Both methods revealed that P and K were the elements most commonly limiting to growth at this site. Although the addition of 113 kg P ha^{-1} and 77 kg K ha^{-1} (Table 3.4) over the four-year period may have alleviated the limitation of these nutrients to an extent, these fertiliser applications were not sufficient to entirely eliminate these particular nutrient constraints. In addition, Bainbridge *et al*. (1995) have demonstrated that highly weathered clay soils in this region of South Africa have the highest P-sorption capacities, and therefore significantly more P would need to be applied to fully overcome this particular property of the soil.

9.5 OVERVIEW

Silvicultural practices that can potentially improve immediate nutrient availability to trees (e.g. fertilisation), are highly likely to have the greatest effect on leaf area development, and hence growth, during the early stages of stand establishment (du Toit and Dovey, 2005). Leaf area index is by far the most important canopy characteristic because it is a fundamental ecophysiological variable that influences the amount of radiation a canopy can intercept and because of its importance in transpiration (Landsberg and Gower, 1997).

Initial leaf area development in an *E. grandis* trial in the KwaZulu-Natal Midlands responded strongly to a nutrient availability gradient produced by site management treatments (du Toit and Dovey, 2005). The application of fertiliser to *E. grandis* trees in Australia resulted in a more rapid expansion of initial leaf area during crown development (Cromer *et al*., 1993b). Similarly, in this irrigation and fertilisation trial, initial *L* responded to an enhanced nutrient supply mediated through fertilisation. At age two years, the *L* in fertilised (F and IF) trees was 3.8 compared to 3.0 in trees that did not receive additional nutrients (C and I). At three years, the corresponding values were 5.2 (F and IF) and 4.1 (C and I). This fertiliser effect was weakly significant (p = 0.06 at age two years and p = 0.06 at three years). At age four years, however, an increase in water availability in contrast to nutrient supply accounted for the *L* response. At this stage, irrigation produced significantly (p = 0.04) higher *L* values of 4.8 (I and IF) in comparison to 4.4 in those trees that were not irrigated (C and F).

After canopy closure, improved nutrition will have a less marked effect on *L*, resulting from potential limitations arising from soil water availability (du Toit and Dovey, 2005). In short-rotation plantations which are generally limited by soil water availability, du Toit and Dovey (2005) suggest that the window of opportunity to improve productivity lies in the early stages of stand growth, before leaf area development is constrained by soil water limitations. The significant response of *L* to irrigation at four years indicates that at this stage of stand development, soil water availability is potentially more limiting than nutrients at this site.

Site water balance has an overriding influence on the growth responses that are possible through manipulation of the soil nutrient supply (Nambiar and Brown, 1997). It is possible that tree growth at this site was initially constrained by site factors (nutrition) and over time, climatic effects (water supply) became more limiting. It was hypothesised that in young trees, limited transpiration occurred because of a low leaf area, and growth was then restricted by nutrients because of the low water demand. As the stand continued to develop and leaf area reached a peak value, the high transpiration demand could not be met by the current soil moisture status, and the water demand exceeded the nutritional requirement.

Irrigation and fertiliser application appeared to relieve the potential water and nutrient limitations at this site, but neither of these resources were completely eliminated as growth-limiting factors. Therefore, potential forest yields could not be demonstrated. This trial highlights the importance of good establishment practices, appropriate vegetation control and adequate nutrition in the initial survival and growth of eucalypt seedlings, which have the potential to be carried throughout the rotation.

CHAPTER 10

CONCLUSIONS

The growth of the *E. grandis* trees in this trial was constrained by poor establishment and management practices. Inadequate vegetation control and vigorous weed growth caused a marked competition in the establishment of the seedlings. In addition, the variable seed stock and damage from animals resulted in late canopy closure. Consequently, the potential growth of *E. grandis* at this site could not be determined, and comparisons were made between the different treatments rather than demonstrating maximum growth under optimal conditions.

Appropriate data were collected to address the objectives and key questions presented in Chapter 1. The stated objectives have, to a large extent, been met. With respect to the first objective and key question, the results from this trial suggest that there was an apparent temporal separation of resource limitation experienced by the trees. During the early stages of stand development, the trees appeared to be constrained by nutrient availability, whereas water was potentially more limiting to growth than nutrient supply at four years of age.

The second objective and associated key questions were addressed by quantifying the biomass and N and P pools contained in the various components of this *E. grandis* stand. At age four years, irrigation had a more pronounced effect on growth and biomass accumulation than fertiliser addition. Increases in DBH, tree height, BA, standing volume, and above- and below-ground biomass were observed in response to increased water availability. Significantly more above-ground biomass was allocated to the stems of irrigated (I and IF) trees, and fertiliser application resulted in proportionally less mass being allocated to below-ground components compared to non-fertilised trees. The highest N and P accumulation in above- and below-ground biomass components occurred in response to irrigation.

A model validation exercise was conducted to address the third objective and key question by testing *L*, foliage and above-ground woody biomass, and stand volume predictions by 3-PG. Evaluation of 3-PG model outputs against field measurements indicated a generally good correlation for growth data across the C, I, F and IF trees. Stand volume at four years of age was under-predicted in the non-irrigated treatments. Actual stand volume at this age ranged from 100 to 118 m^3 ha^{-1} across all treatments, compared to model estimates of 79 to 121 m^3 ha^{-1}. Outputs from the 3-PG model have highlighted the need to focus our understanding on how *FR* varies seasonally and with silvicultural regime to provide an objective method for estimating *FR* values. Dynamic allocation patterns between above- and below-ground components in response to site resource availability deserve further investigation. The results have shown 3-PG to be a robust model, producing accurate predictions of tree growth under varying levels of resource availability, using a single parameter set. It is encouraging that the model can predict canopy response (in terms of leaf area) to changes in resource availability, as this is the tree component that ultimately drives growth and water use.

The water use of an *E. grandis* tree growing under conditions of non-limiting soil water was quantified to address the fourth objective and associated key questions. Daily sap flow rates were recorded in a single irrigated (I) tree, and were used to estimate mean daily g_c. Analysis of daily and seasonal variation in conductance confirmed that solar radiation and *D* are the dominant factors reducing g_c below potential values, when soil water availability is high. A simple g_c model was developed, based on these data, and used in combination with the P-M equation to predict daily transpiration rates by *E. grandis* trees at a second site situated in Mpumalanga. Transpiration estimated using the P-M equation and g_c model agreed well with the observed daily sap flow (R^2 = 0.79). Mean daily transpiration at the Mpumalanga site was 3.4 mm, with a maximum of 6.8 mm. These values lie well within the range of water use estimates cited for *E. grandis*.

The fifth objective and relevant key questions were addressed by generating DRIS norms for N, P, K, Ca and Mg from published *E. grandis* data and comparing these to foliar target levels recommended by Linder (1995) for optimal growth. The data bank used to generate the norms was much smaller than initially expected, and DRIS norms for the micronutrients could not be developed. The DRIS norms for P and K relative to N corresponded to the target values, but the Ca:N and Mg:N ratios were much higher, indicating luxury consumption of these elements. A similar trend was observed by

Knecht and Göransson (2004), who calculated foliar nutrient ratios from published data on a wide range of plant species. The DRIS norms were used to evaluate the nutrient balance in the C, I, F and IF treatments, and to demonstrate changes in the relative nutrient status following fertiliser application. In most cases, the diagnosis made using the DRIS indices was confirmed with the optimal ratio approach. The DRIS appears useful for diagnosing the nutrient status, provided accurate DRIS norms are used and indices are interpreted correctly. Diagnoses made using the optimal ratio approach and the DRIS technique indicated that foliar levels of P and K were sub-optimal at age four years.

The results from this trial have indicated that water is potentially more limiting to growth than nutrient supply at four years of age. However, it is highly unlikely that irrigation of forest species would ever be implemented on an operational scale in this water-limited country. Rather than pursuing the potential responses that could be obtained with unlimited water availability, improved fertiliser recommendations would be most beneficial for the forest industry in South Africa. On the basis of the DRIS indices, in combination with the optimal nutrient ratio approach, it is suggested that maintaining the foliar ratios at levels of 100 N: 8 P: 35 K: 2.5 Ca: 4 Mg will result in optimal growth of *E. grandis* trees, provided no other resources are limiting.

CHAPTER 11

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APPENDIX 1

FOLIAR NUTRIENT RATIOS IN THE RESPECTIVE HIGH- AND LOW-YIELDING SUB-POPULATIONS, USED IN THE CALCULATION OF THE DRIS NORMS PRESENTED IN CHAPTER 8

Ref. no.	HIGH-YIELDING SUB-POPULATION																			
	N:P	P:N	N:K	K:N	N:Ca	Ca:N	N:Mg	Mg:N	P:K	K:P	P:Ca	Ca:P	P:Mg	Mg:P	K:Ca	Ca:K	K:Mg	Mg:K	Ca:Mg	Mg:Ca
1	18.0	0.06	3.5	0.29	2.8	0.36	8.0	0.13	0.20	5.0	0.15	6.7	0.43	2.3	0.75	1.3	2.1	0.47	3.3	0.30
2	13.3	0.08																		
3	11.9	0.08																		
4	14.0	0.07																		
5	13.0	0.08	3.0	0.33	2.0	0.50	6.7	0.15	0.22	4.5	0.16	6.5	0.52	1.9	0.70	1.4	2.3	0.43	3.3	0.30
6	11.3	0.09	3.0	0.34	2.8	0.35	8.2	0.12	0.26	3.8	0.25	4.0	0.72	1.4	0.95	1.1	2.8	0.36	2.9	0.35
7	9.1 15.1	0.11 0.07	1.8 2.6	0.56 0.38	3.0 1.8	0.34 0.57	9.4 7.3	0.11 0.14	0.20 0.17	5.1 5.8	0.33 0.12	3.1 8.6	1.04 0.48	1.0 2.1	1.66 0.67	0.6 1.5	5.3 2.8	0.19 0.35	3.2 4.2	0.31 0.24
8	10.9 9.7 9.5	0.09 0.10 0.11																		
9	13.1 8.6	0.08 0.12																		
10	14.2	0.07																		
11	10.5	0.10	1.7	0.58	3.7	0.27	8.3	0.12	0.16	6.1	0.35	2.8	0.79	1.3	2.15	0.5	4.8	0.21	2.2	0.45
12	11.6 11.4	0.09 0.09																		
13	8.5 10.2	0.12 0.10	2.8 3.6	0.36 0.28					0.33 0.35	3.1 2.9										
14	18.8	0.05	3.9	0.26	5.9	0.17	15.1	0.07	0.21	4.8	0.32	3.2	0.80	1.3	1.53	0.7	3.9	0.26	2.5	0.39
15	23.2	0.04	3.7	0.27	7.5	0.13	9.3	0.11	0.16	6.3	0.32	3.1	0.40	2.5	2.03	0.5	2.5	0.40	1.2	0.81
16	16.3	0.06	2.3	0.43	4.0	0.25	8.0	0.13	0.14	7.0	0.25	4.1	0.49	2.0	1.73	0.6	3.5	0.29	2.0	0.50

APPENDIX 1 (continued)

Ref. no.	LOW-YIELDING SUB-POPULATION																		
	N:P	P:N	N:K	K:N	N:Ca	Ca:N	N:Mg	Mg:N	P:K	K:P	P:Ca	Ca:P	P:Mg	Mg:P	K:Ca	Ca:K	K:Mg	Mg:K	Ca:Mg	Mg:Ca
6	3.2	0.31	1.7	0.59	1.0	0.97	6.1	0.17	0.53	1.9	0.32	3.1	1.89	0.5	0.61	1.6	3.6	0.28	5.9	0.17
	10.5	0.10	2.2	0.45	2.7	0.37	19.8	0.05	0.21	4.7	0.26	3.9	1.89	0.5	1.22	0.8	8.9	0.11	7.3	0.14
	18.8	0.05	2.2	0.46	1.9	0.53	7.3	0.14	0.11	8.7	0.10	9.9	0.39	2.6	0.88	1.1	3.4	0.30	3.8	0.26
	8.1	0.12	4.8	0.21	1.9	0.53	7.3	0.14	0.59	1.7	0.24	4.3	0.90	1.1	0.40	2.5	1.5	0.65	3.8	0.26
	7.5	0.13	1.8	0.55	2.6	0.38	4.7	0.21	0.24	4.2	0.35	2.9	0.63	1.6	1.45	0.7	2.6	0.38	1.8	0.55
7	7.2	0.14	1.3	0.79	2.1	0.47	6.5	0.15	0.17	5.7	0.29	3.4	0.89	1.1	1.68	0.6	5.1	0.20	3.0	0.33
	10.4	0.10	2.0	0.51	3.6	0.28	8.7	0.11	0.19	5.3	0.34	2.9	0.83	1.2	1.82	0.5	4.4	0.23	2.4	0.41
	7.6	0.13	1.3	0.75	1.7	0.58	3.8	0.26	0.18	5.7	0.23	4.4	0.50	2.0	1.30	0.8	2.8	0.35	2.2	0.46
	11.4	0.09	1.7	0.58	4.1	0.24	8.0	0.13	0.15	6.7	0.36	2.8	0.70	1.4	2.41	0.4	4.7	0.21	1.9	0.52
	5.2	0.19	1.1	0.88	1.7	0.60	3.5	0.28	0.22	4.5	0.33	3.1	0.68	1.5	1.48	0.7	3.1	0.32	2.1	0.48
	5.0	0.20	1.1	0.91	1.7	0.60	4.3	0.23	0.22	4.5	0.33	3.0	0.86	1.2	1.51	0.7	3.9	0.26	2.6	0.39
	5.1	0.20	1.0	0.97	1.5	0.68	4.0	0.25	0.20	4.9	0.29	3.5	0.79	1.3	1.41	0.7	3.9	0.26	2.8	0.36
	13.3	0.08	2.7	0.37	2.1	0.47	6.0	0.17	0.20	4.9	0.16	6.3	0.45	2.2	0.78	1.3	2.2	0.45	2.8	0.35
	10.6	0.09	1.6	0.61	3.8	0.27	8.2	0.12	0.15	6.5	0.35	2.8	0.77	1.3	2.29	0.4	5.0	0.20	2.2	0.46
	8.1	0.12	1.9	0.52	2.1	0.48	3.8	0.27	0.24	4.2	0.26	3.8	0.46	2.2	1.10	0.9	2.0	0.51	1.8	0.56
	6.9	0.14	0.9	1.14	1.4	0.70	4.7	0.21	0.13	7.9	0.20	4.9	0.68	1.5	1.63	0.6	5.4	0.19	3.3	0.30
	5.2	0.19	0.6	1.73	1.0	0.96	3.1	0.32	0.11	9.0	0.20	5.0	0.60	1.7	1.80	0.6	5.4	0.19	3.0	0.33
8	13.7	0.07																		
	9.1	0.11																		
	10.3	0.10																		
9	29.2	0.03																		
	11.5	0.09																		
10	12.6	0.08																		
	8.7	0.11																		
	9.7	0.10																		
	10.5	0.10																		
11	4.8	0.21	2.2	0.45	0.9	1.08	3.2	0.32	0.46	2.2	0.19	5.2	0.66	1.5	0.42	2.4	1.4	0.70	3.4	0.29
	7.9	0.13	1.6	0.61	1.1	0.87	4.5	0.22	0.21	4.8	0.15	6.9	0.58	1.7	0.69	1.4	2.8	0.36	4.0	0.25
	6.9	0.15	1.4	0.70	1.1	0.89	4.4	0.23	0.21	4.8	0.16	6.1	0.65	1.6	0.79	1.3	3.1	0.32	3.9	0.25
	7.9	0.13	1.4	0.73	1.5	0.65	5.1	0.20	0.17	5.8	0.20	5.1	0.65	1.6	1.13	0.9	3.7	0.27	3.3	0.30

APPENDIX 1 (continued)

Ref. no.	LOW-YIELDING SUB-POPULATION																		
	N:P	**P:N**	**N:K**	**K:N**	**N:Ca**	**Ca:N**	**N:Mg**	**Mg:N**	**P:K**	**K:P**	**P:Ca**	**Ca:P**	**P:Mg**	**Mg:P**	**K:Ca**	**Ca:K**	**K:Mg**	**Mg:K**	**Ca:Mg**	**Mg:Ca**
11	7.6	0.13	1.5	0.67	1.5	0.67	4.7	0.21	0.20	5.1	0.20	5.1	0.62	1.6	1.00	1.0	3.1	0.32	3.1	0.32
	7.9	0.13	1.4	0.72	1.5	0.65	5.1	0.20	0.18	5.7	0.20	5.1	0.65	1.6	1.12	0.9	3.7	0.27	3.3	0.30
	9.2	0.11	1.8	0.56	1.6	0.64	5.3	0.19	0.19	5.2	0.17	5.8	0.58	1.7	0.89	1.1	3.0	0.33	3.4	0.30
	12.2	0.08	2.2	0.45	2.5	0.39	8.0	0.13	0.18	5.5	0.21	4.8	0.66	1.5	1.15	0.9	3.6	0.28	3.1	0.32
	9.1	0.11	1.9	0.53	1.7	0.60	5.9	0.17	0.21	4.9	0.18	5.5	0.65	1.6	0.88	1.1	3.1	0.32	3.5	0.28
	11.0	0.09	2.2	0.45	2.2	0.45	7.3	0.14	0.20	5.0	0.20	5.0	0.67	1.5	1.01	1.0	3.3	0.30	3.3	0.30
12	10.4	0.10	2.2	0.46					0.21	4.8										
	14.7	0.07	2.8	0.36					0.19	5.2										
13	6.6	0.15	2.1	0.47					0.32	3.1										
14	17.9	0.06	5.2	0.19	4.8	0.21	13.1	0.08	0.29	3.5	0.27	3.7	0.73	1.4	0.93	1.1	2.5	0.39	2.7	0.37
15	19.7	0.05	4.9	0.20	4.2	0.24	11.4	0.09	0.25	4.0	0.21	4.7	0.58	1.7	0.85	1.2	2.3	0.43	2.7	0.37
	24.3	0.04	4.7	0.21	6.1	0.16	11.4	0.09	0.20	5.1	0.25	4.0	0.47	2.1	1.28	0.8	2.4	0.41	1.9	0.53
	22.1	0.05	5.2	0.19	5.1	0.20	11.7	0.09	0.24	4.2	0.23	4.3	0.53	1.9	0.97	1.0	2.2	0.45	2.3	0.44
	22.5	0.04	5.5	0.18	3.6	0.28	12.0	0.08	0.24	4.1	0.16	6.3	0.53	1.9	0.66	1.5	2.2	0.45	3.3	0.30
17	23.8	0.04	4.0	0.25	1.6	0.63	5.9	0.17	0.18	5.5	0.06	15.6	0.25	3.9	0.35	2.8	1.4	0.72	3.9	0.25

NOTE: 1. The references used in compiling this data bank are listed on pages 144 – 147.
2. In cases where multiple nutrient ratios are listed for a single reference, this indicates that the particular study included a number of treatments and/or trees of different ages.
3. Blank cells in the table indicate that no information was available for the particular nutrient ratio.

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NOTE: 1. In cases where multiple references are listed, this includes all the available literature relevant to a particular study.

APPENDIX 2

PUBLISHED PAPERS